Communiquer entre espèces pour faire face au prédateur : le cas des cris de harcèlement chez les passereaux

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Communiquer entre espèces pour faire face au prédateur : le cas des cris de harcèlement chez les passereaux

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« Expliquer, comprendre, pénétrer quelque chose au moins du mystère du monde, il n'est pas, dans le domaine des choses de l'esprit, de joie plus solide et de plus enivrant bonheur que d'avoir pu, fût-ce une seule fois, dans le plus humble domaine et sur le plus infime détail, y parvenir. »

Théodore Monod

Avant-propos

Ce travail de thèse correspond à la succession de différentes histoires personnelles et intellectuelles. Mon travail sur l'étude du comportement de harcèlement a débuté en Master 2, ou peut-être avait-il déjà pris racine en Master 1 durant mon stage sur la communication chez la chouette chevêche (*Athene noctua*) sous la direction de Thierry Lengagne. A la suite de l'obtention de résultats forts sympathiques traitant de l'impact de la chevêchette d'Europe sur le comportement de harcèlement des passereaux, j'ai eu la chance de poursuivre ce travail en thèse. Thèse qui a bénéficié d'un financement de thèse du Ministère de la Recherche française via l'Ecole Doctorale E2M2 de l'Université Claude Bernard Lyon 1. Mais voilà, les idées, les questions fusaient… Dès lors, comment raconter au lecteur une histoire homogène puisque ce travail de thèse s'articule autour de plusieurs questions.

L'envie d'apprendre et de découvrir des savoirs ne m'ont pas lassée durant ces trois années. Et, au contraire, c'est en partie de ma faute si certains résultats s'écartent du chemin initial. Il faut dire que 36 modèles d'études se prêtaient particulièrement bien à cet aspect !

Finalement, nos questions étaient diverses et variées mais elles étaient avant tout complémentaires et s'articulaient autour d'un même point d'encrage. La présente thèse est donc structurée en trois sections : la première pose le cadre théorique, la deuxième comprend les articles publiés, acceptés, ou en préparation et la troisième correspond à la discussion générale. J'ai voulu offrir au lecteur tout au long de ce manuscrit une histoire complète s'articulant autour d'un thème principal, la communication entre des espèces de passereaux dans le cas du harcèlement d'un prédateur.

Remerciements

Nous parlons « d'exercice des remerciements » mais ne devrions-nous pas simplement évoquer le plaisir de remercier les gens qui nous accompagnent tout au long d'un cursus formidable de la vie ? quel qu'il soit…

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Les données récoltées sur le terrain ne sont pas le fruit d'une seule personne et je tiens à remercier l'ensemble des stagiaires qui m'ont aidé durant ces trois années. Cette thèse a été *un travail de terrain énorme la première année. Après 3480 km parcourus à pied, 1419 oiseaux testés…une grande réussite ! Merci à Alexandra Christin, Carole Gros, Marilou Angénieux, Yacine Aissi, Juliette Berger, Caroline Blanc-Billard, Gwendoline Guerro et Léo Maucourt (promo 2016). N'épargnant ni votre temps ni vos efforts, vous avez été les auteurs d'un grand nombre d'observations contenues dans cette thèse. Deuxième année, le terrain colossal n'aurait pas été accompli sans le travail d'une équipe de stagiaires exemplaires ! Merci à Alice Rouffy, Laurène Demange, Margaux Sevestre, Camille Locatelli, Michaël Girard, Justine Huvelin et Anne Pandraud. Merci à eux pour tout le travail réalisé. Troisième année, merci à Solène Bischoff, Amélie Héraud et Nathan Gellé pour tout le travail accompli. Merci à vous tous pour votre enthousiasme et votre bonne humeur. J'ai pris un réel plaisir à travailler en votre compagnie.*

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-SOMMAIRE-

Résumé

L'utilisation des signaux acoustiques permet aux animaux d'échanger des informations importantes que ce soit pour leur reproduction ou pour leur survie. L'essentiel des études réalisées concerne la communication entre congénères mais un certain nombre ont mis en évidence l'utilisation d'informations acoustiques entre espèces différentes. Alors que dans la plupart des cas les proies fuient le prédateur et émettent des cris d'alarme pour chercher à se mettre hors de portée du prédateur, elles s'approchent parfois de lui pour provoquer son départ. Ce comportement de harcèlement s'accompagne de l'émission d'un signal de harcèlement hétérospécifique car très vite de nombreuses espèces viennent harceler le prédateur.

L'objectif de mon travail de thèse est de comprendre comment est régi le transfert d'informations entre plusieurs espèces de passereaux dans le cas du comportement de harcèlement d'un prédateur. Ces travaux mettent en évidence que le comportement de harcèlement des passereaux face à la chouette chevêchette (*Glaucidium passerinum*) (i) est spécifique à cette espèce de chouette prédatrice de passereau, (ii) disparait lorsque la chouette n'est plus présente et (iii) est d'autant plus intense que l'espèce appartient au régime alimentaire de la chouette. Par ailleurs, les résultats indiquent un transfert d'informations entre les espèces et mettent en évidence une propension variable des différentes espèces à se rallier autour du harceleur.

Les différents jeux d'expérience de repasse réalisés sur le terrain m'ont permis d'étudier les mécanismes impliqués dans le transfert d'informations et la reconnaissance des cris de harcèlement. Mon travail montre que les variations de réponses aux cris de harcèlement émis par les individus hétérospécifiques peuvent dépendre de la similarité acoustique, des relations interspécifiques et des variations saisonnières. Néanmoins, la complexité du système de communication chez de nombreuses espèces de passereaux nous empêche probablement de trouver un phénomène général applicable à toutes les espèces. Mes résultats indiquent également que la connaissance préalable des signaux de harcèlement n'est pas forcément nécessaire pour répondre aux cris puisque que trois espèces de Paridé européens ont répondu à des cris de harcèlement d'oiseaux américains. Nous montrons cependant qu'un processus d'apprentissage associatif favorise la mise en place de la réponse aux cris. Cette thèse suggère également qu'il y a une évolution convergente sur la largeur de bande de fréquence des cris de harcèlement. Ce type de structure permet une localisation rapide de l'émetteur, ce qui est indispensable pour rameuter des proies potentielles lors du harcèlement. Enfin, mon travail indique que le codage de l'information dans les cris de harcèlement repose sur une combinaison de deux types d'appels et que les passereaux sont sensibles à l'ordre dans lequel ces appels sont combinés.

L'ensemble de ces avancées nous oblige désormais à considérer la communication acoustique chez les passereaux en prenant en compte le risque de prédation, les interactions hétérospécifiques et la complexité des signaux acoustiques.

Mots clés : attraction hétérospécifique, communication acoustique, comportement de harcèlement, passereaux, stratégie anti prédatrice.

Champ disciplinaire : **Écologie comportementale**

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Introduction générale

I / La communication acoustique

1) La communication

Dans le règne animal, l'ensemble des interactions entre individus implique un phénomène de communication (Hauser 1996). Cette communication génère des comportements qui sont parmi les plus spectaculaires et les plus intrigants que l'on puisse observer. Qu'il s'agisse du chant des baleines ou du hurlement des loups, rares sont les observateurs qui restent indifférents face à des animaux qui communiquent.

La communication constitue un comportement complexe au cours duquel des informations contenues dans le signal émis par un individu (l'émetteur), vont être utilisées par un autre individu (le récepteur) lui permettant de prendre une décision (Shannon & Weaver 1949, Marler 1967, Otte 1974, Krebs & Davies 1983) (Figure 1). Les informations sont portées par des signaux de diverses natures (acoustiques, visuels, électriques ou chimiques) qui sont transmis au récepteur *via* un canal de transmission (Figure 1). Le canal de transmission peut être défini comme le milieu physique (air, eau, sol…) servant de support au transfert de l'information, i.e. l'environnement et ses « obstacles ». En fonction de l'espèce et du contexte d'émission, plusieurs canaux de communication peuvent être utilisés en même temps, on parle alors de communication multimodale (Partan 1999). Chaque type de signal a ses propres propriétés en termes de propagation, vélocité et coûts énergétiques. Les signaux acoustiques ont la particularité de se propager sur de courtes ou longues distances et d'être efficaces de jour comme de nuit, en milieu faiblement éclairé ou encombré (ex. végétation dense) à l'inverse des signaux visuels (Catchpole & Slater 2003). Contrairement aux signaux chimiques, les signaux acoustiques et visuels ont une vélocité élevée, peuvent être directionnels et ne laissent pas de trace dans l'environnement (Sparks 1984, Simmons 2003, Davies et al. 2012).

D'un point de vue théorique, il est attendu que les pressions de sélections favorisent les signaux permettant de diminuer l'incertitude dans la décision prise par le récepteur (Guilford & Dawkins 1991). En d'autres termes, on s'attend à ce qu'un signal évolue de manière à ce que la réponse observée soit la plus proche possible de celle attendue. Les signaux seraient produits par l'émetteur pour manipuler le comportement du récepteur afin d'en tirer des bénéfices (Dawkins & Krebs 1978). Dans ce cas, le signal évoluerait de manière à porter des informations « trompeuses » menant à une réponse potentiellement inadaptée pour le récepteur dont l'émetteur pourra tirer des bénéfices. Mais en contrepartie, la sélection favorisera des récepteurs qui sont capables de discerner la nature et les intentions des émetteurs résistant ainsi à la manipulation. Les récepteurs exercent sur les émetteurs une double pression sélective qui favorise la production de signaux codant une information fiable et clairement discriminable (Guilford & Dawkins 1991).

Dans certains cas l'information peut être détournée par un récepteur indésirable. En particulier, l'information publique, aussi connue sous le nom d'écoute clandestine (*eavesdropping*), se produit lorsqu'un individu autre que le destinataire prévu utilise l'information contenue dans le signal.

Pour que la communication soit qualifiée de « communication vraie », il est nécessaire que les intérêts des individus qui communiquent convergent, c'est-à-dire que le partage d'informations bénéficie à l'émetteur et au récepteur (Simmons 2003).

Historiquement, les études menées sur la communication concernaient la communication entre congénères (i.e. le récepteur de l'information est un individu de la même espèce que l'émetteur). La communication intraspécifique, extrêmement répandue dans le monde animal, est utilisée dans de nombreux contextes. De façon générale, tous sont liés à des interactions sociales comme le choix du partenaire ou la compétition sexuelle, les soins aux jeunes, la coopération réciproque ou l'altruisme vrai. La découverte, à partir des années 1990, de la communication hétérospécifique, a permis d'ouvrir un nouveau champ de recherche. La communication hétérospécifique, récemment envisagée, concerne des signaux qui fournissent au récepteur des informations sur un émetteur hétérospécifique. Ces informations concernent souvent des ressources accessibles comme de la nourriture ou des prédateurs.

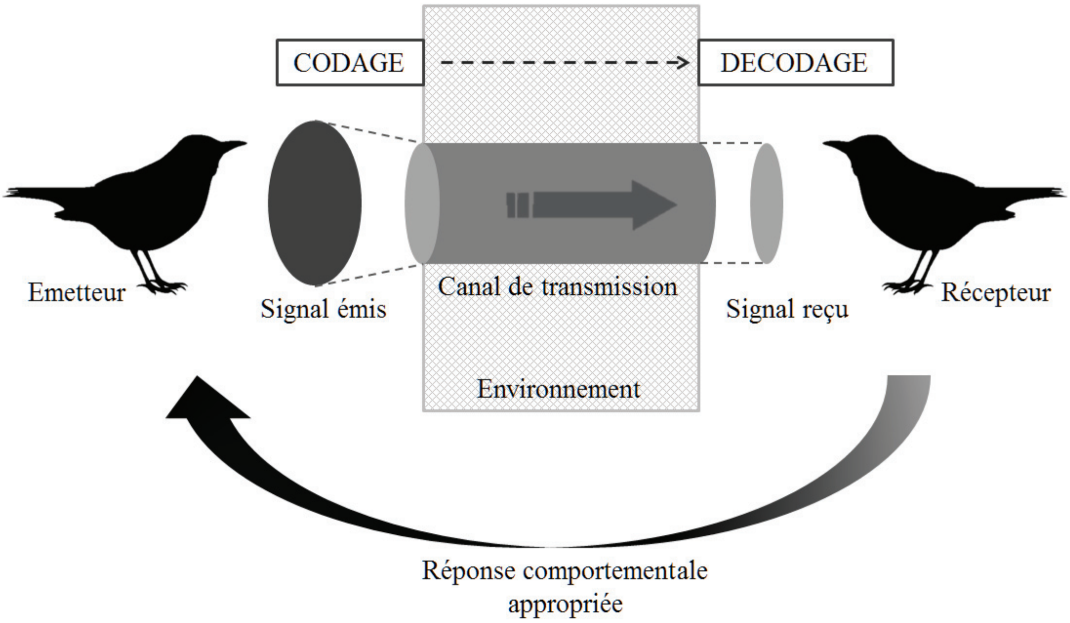

Figure 1 : Chaine de transmission de l'information. Un signal codant de l'information est échangé entre un individu émetteur et un récepteur. Durant sa transmission, le signal subira des modifications diminuant la qualité de l'information portée. Le récepteur décodera le signal reçu afin d'extraire l'information et répondre à l'aide d'un comportement approprié.

2) Le cas de la communication acoustique

a) La production du signal

La communication acoustique, que l'on trouve uniquement chez les Arthropodes et les Vertébrés, est particulièrement développée chez les espèces se déplaçant dans les trois dimensions de l'espace : insectes, mammifères marins, chiroptères, primates et oiseaux (Brown & Farabaugh 1997, Beecher & Brenowitz 2005) et a donné lieu à l'évolution d'appareil de production spécialisé propre à chaque groupe : les organes vibratoires chez les insectes, le larynx chez les mammifères et la syrinx chez les oiseaux. Il est généralement admis que chacun de ces appareils vocaux a évolué en relation avec les contraintes environnementales et énergétiques (Gridi-Papp et al. 2006). Chez les vertébrés, chaque système de production comprend trois éléments : un système générant un flux d'air, un mécanisme vibratoire et une cavité de résonnance. Chez les oiseaux, la syrinx est constituée de deux demi-syrinx fonctionnant indépendamment l'une de l'autre (« théorie des deux voix »; Nottebohm 1971, Lemon 1973, Suthers 1994) permettant de produire des structures acoustiques très variées codant diverses informations. Les oiseaux sont capables de contrôler leur syrinx avec une précision inférieure à la milliseconde. La structure de la syrinx présente des variations interspécifiques (Hauser 1996) permettant de distinguer les oscines (i.e. les oiseaux/passereaux chanteurs) des suboscines (i.e. les oiseaux/passereaux non chanteurs et les non passereaux). Son fonctionnement est particulièrement complexe chez les oiseaux chanteurs (Düring et al. 2013). Les oiseaux constituent l'un des groupes de prédilection pour étudier l'ontogénèse de la communication vocale car ils présentent de nombreux points communs (apprentissage des vocalisations, syntaxe, processus neuronal…) avec l'homme (Riede & Goller 2010, Lipkind et al. 2013).

b) Les informations transmises par la communication acoustique chez les oiseaux

Certainement dû au fait de leur système de production complexe, leur grande diversité et des nombreuses stratégies reproductives et anti-prédatrices, un grand nombre d'études ont été réalisées chez les oiseaux qui ont développé un mode de communication parmi les plus élaborés (Catchpole & Slater 2003). Grâce à la communication acoustique, les oiseaux transmettent des informations très diverses à destination des conspécifiques ou des hétérospécifiques. Les signaux acoustiques peuvent contenir des marqueurs géographiques pouvant jouer un rôle dans l'appariement ou être considérées comme simple marqueur de population (Bretagnolle & Lequette 1990). Beaucoup d'études ont également été menées sur l'information individuelle contenue dans le signal acoustique (e.g. Lengagne et al. 2001).

c) Classification des émissions sonores chez les oiseaux

L'ensemble des émissions sonores est réparti suivant leurs fonctions et leurs structures : les chants et les cris. En général, les chants sont plus longs et ont une structure plus complexe par la richesse et les variétés de formes des éléments qui les composent (Catchpole & Slater 2003). Chez de nombreuses espèces tropicales, le mâle et la femelle produisent des chants pendant toute l'année, tandis que chez la plupart des espèces des zones tempérées, les chants sont produits uniquement par le mâle pendant les quelques mois de la saison de reproduction (Collins 2004). Les chants font partie intégrante du comportement territorial qui vise à écarter les compétiteurs de même sexe (généralement mâle) de la ressource à défendre (i.e. territoire). La possession d'un territoire s'avère cruciale pour la reproduction et la survie chez la plupart des espèces d'oiseaux. Les chants territoriaux visent également à attirer un partenaire sexuel (Collins 2004). Les cris, quant à eux, tendent à être plus courts, moins complexes et sont produits par les deux sexes tout au long de l'année dans des contextes plus variés. Chez les oscines, les chants sont généralement appris alors que les cris sont souvent considérés comme innés (Catchpole & Slater 2003).

3) Les systèmes de codage et décodage de l'information

Le codage et le décodage de l'information véhiculée par le contenu du signal sont généralement basés sur des caractéristiques sonores résistantes à la propagation et adaptées aux exigences biologiques de l'espèce dans son environnement (Aubin & Brémond 1983, Aubin & Mathevon 1995). Deux caractéristiques des signaux sonores peuvent permettre d'encoder/décoder de l'information : les caractéristiques spectrales et/ou les caractéristiques temporelles (Okanoya & Dooling 1991). Le contenu spectral correspond à la distribution d'énergie dans le domaine fréquentiel. Des paramètres comme la fréquence minimale ou la fréquence maximale du signal permettant de décrire le domaine fréquentiel sont souvent mesurés (e.g. Lengagne 2001, Dahl & Gary Ritchison 2018). L'individu peut également utiliser un système basé sur une analyse temporelle des caractéristiques du signal (Becker 1982) en tenant compte de la distribution de l'énergie dans le domaine temporel permettant de définir des unités (notes ou syllabes). Le codage de l'information peut être basé sur un système d'assemblage d'unités correspondant à un pattern inter-syllabique (e.g. syntaxe = ordre des syllabes ; rythme = durée silence/durée du son ou tempo = nombre syllabes / temps) et/ou se retrouver à l'intérieur même d'une unité. Le pattern intra-syllabique peut être mesuré à partir de la modulation de fréquence ou d'amplitude et des battements générés par les deux voix (e.g. Lengagne et al. 2001).

Ces dix dernières années, un certain nombre d'études se sont penchées sur une potentielle utilisation de la syntaxe chez les mammifères et les oiseaux. La syntaxe est souvent considérée comme l'une des principales caractéristiques du langage humain (Hurford 2011). Elle correspond à une combinaison de mots significatifs (i.e. ayant un sens) formant une plus grande séquence complexe (Hockett 1960, Marler 1998). Bien que de plus en plus d'études utilisent le terme syntaxe pour qualifier le système de codage de certaines espèces, la capacité des animaux à utiliser la syntaxe compositionnelle reste largement débattue (Petkov & Jarvis 2012, Petkov & Wilson 2012, Bolhuis et al. 2018). A l'heure actuelle, il est difficile de savoir dans quelle mesure cette syntaxe est répandue chez les oiseaux (Russell & Townsend 2017, Griesser et al. 2018).

La façon dont des informations identiques (menace, risque de prédation) peuvent être codées varie entre les espèces. Par exemple, une récente étude comparant les signaux émis par six espèces de mésanges indique que ces espèces n'utilisent pas le même pattern inter-syllabique (Carlson et al. 2017a). Dans certains cas les récepteurs montrent une grande souplesse dans le décodage des informations dégradées (e.g. Park & Dooling 1986). Pour faire face aux signaux dégradés, les animaux peuvent se concentrer sur des caractéristiques acoustiques susceptibles d'être moins dégradées par la propagation. Par exemple, la mouette rieuse (*Larus ridibundus*) ne tient pas en compte la modulation d'amplitude dans le processus de décodage des appels de détresse; cela semble être bien adapté à la transmission à longue distance puisque la modulation d'amplitude est toujours sujette à de fortes dégradations (Brémond & Aubin 1992). Enfin, le décodage de l'information dépend également des conditions psycho-physiologiques de l'individu (par exemple le stress ou l'état reproducteur altèrent la perception des informations ; Cummings et al. 2008, Schulz et al. 2013).

4) Évolution du signal acoustique

Au cours des dernières décennies, un grand effort a été fait pour comprendre l'évolution de la communication acoustique dans différents taxons. Le rôle de la sélection sexuelle et de la sélection naturelle dans l'évolution des signaux acoustiques a fait l'objet de nombreux travaux. La divergence des signaux joue un rôle clé dans le cas où les individus doivent établir et maintenir de l'isolement reproducteur (Slabbekoorn & Smith 2002). Dans le cas où les individus seraient amenés à partager des informations, les forces exercées sur le signal conduiraient les individus produisant le signal à trouver une solution acoustique commune (convergence des signaux).

Trois principales sources de divergence ou de convergence acoustique non exclusives sont généralement avancées pour expliquer l'évolution de la communication acoustique (Wilkins et al. 2013) : i) la sélection en fonction des supports fonctionnels des signaux acoustiques (i.e. le type d'émissions sonores, il peut s'agir d'un type de cri d'alarme ou d'un chant territorial), ii) la sélection environnementale indirecte affectant des traits impliqués dans la production des vocalisations et iii) la dérive (Irwin et al. 2008).

La « fenêtre acoustique » au sein de laquelle les signaux acoustiques peuvent évoluer est déterminée par six contraintes principales (Wilkins et al. 2013) :

(1) *les caractéristiques de l'habitat* : l'énergie des signaux propagés tend à être concentrée sur des fréquences permettant l'optimisation de la transmission du signal (i.e.

minimiser l'atténuation et la réverbération) dans un habitat donné (Patten et al. 2004, Braune et al. 2008, Tobias et al. 2010).

(2) *la composition de la communauté* : la présence de membres de la communauté qui produisent des signaux acoustiques peut entraîner une forte sélection divergente/ convergente sur la structure du signal pour éviter les interférences ou pour faciliter la communication entre espèces. La présence de prédateurs ou de parasitoïdes peut également sélectionner un certain type de signal ou encore la perte de signal (Kirschel et al. 2009, Grant & Grant 2010, Tobias et al. 2010).

(3) *le bruit de fond* : adaptation de la structure du signal pour éviter d'être masqués par les interférences causées par des sources biotiques et abiotiques de bruit ambiant (Ryan & Brenowitz 1985, Kirschel et al. 2009, Luther & Derryberry 2012).

(4) *l'histoire phylogénétique* : les traits dérivés ou ancestraux partagés qui ont évolué dans d'autres contextes sociaux ou écologiques peuvent limiter la variation disponible pour l'évolution du signal (Ryan & Brenowitz 1985, Podos 2001).

(5) *la morphologie et la neurophysiologie de l'émetteur* : les signaux acoustiques sont souvent contraints par des limites morphologiques (e.g. forme du bec ou taille du corps) et neurologiques (Podos 2001, Derrybery et al. 2018).

(6) *la morphologie et la neurophysiologie du récepteur* : la morphologie du récepteur (e.g. les structures auditives) et la neurophysiologie (i.e. les structures neurologiques qui affectent les capacités perceptuelles et cognitives) (Römer 1993, Akre et al. 2011).

Ainsi, concernant « l'efficacité » du signal, les pressions de sélections vont d'une part favoriser les signaux dont la propagation à travers le canal de transmission se fait avec un minimum de perte et de dégradation de l'information. A partir de l'écoute de chants provenant d'espèces d'oiseaux de milieux ouverts et de milieux forestiers, Chapuis (1971) a émis l'hypothèse que le chant des oiseaux avait évolué vers des fréquences plus graves en forêt afin d'être transmis de manière efficace à travers le feuillage. En effet, dans des habitats fermés les surfaces de réverbérations et d'absorptions sont plus importantes qu'en milieu ouvert et atténuent de manière importante la propagation des sons à hautes fréquences (Chapuis 1971, Marten & Marler 1977, Wiley & Richards 1978, Brown & Handford 2000). Cette contrainte environnementale sur la propagation du son, formalisée par Morton (1975) sous le terme « hypothèse d'adaptation acoustique », a largement été étudiée dans le cas des chants au sein de différents taxons et selon différentes contraintes environnementales (Ey & Fisher 2009, Roca et al. 2016), en particulier chez les oiseaux pour lesquels des méta-analyses

(Boncoraglio & Saino 2007, Roca et al. 2016) et des analyses phylogénétiques (Derrybery et al. 2018, Pearse et al. 2018) sont maintenant disponibles. Toutes ces études suggèrent un effet modéré de l'habitat sur la divergence du chant des oiseaux sauf pour une caractéristique acoustique spectrale : le pic de fréquence (fréquence à laquelle l'amplitude/énergie est maximale) (Boncoraglio & Saino 2007, Pearse et al 2018).

5) La communication acoustique entre les espèces

La communication acoustique chez les vertébrés a été étudiée depuis longtemps dans le cadre des interactions sociales (i.e. communication intraspécifique). Cependant, un nombre croissant d'études a mis en évidence l'utilisation d'informations acoustiques entre espèces différentes. Si une partie correspond à de l'utilisation d'indice (pas réellement de la communication) l'autre indique clairement qu'il s'agit de communication. Cette communication a été mise en évidence entre différentes espèces du même genre comme chez les mammifères (Windfelder 2001, Russ et al. 2004) ou les oiseaux (Hurd 1996, Magrath et al. 2007, Nolen & Lukas 2009) mais aussi entre espèces appartenant à des taxons différents comme par exemple la communication mammifères-oiseaux (Anne & Rasa 1983) ou encore homme-animal (Mc Connel & Baylis 1985, Spottiswoode et al. 2016). Dans le cadre de la communication acoustique, la majorité des études a porté sur les communautés d'oiseaux. **Cette communication hétérospécifique qui implique le partage et la compréhension d'une information entre espèces différentes est souvent complexe à mettre en évidence et l'évaluation exacte des gains et des coûts tant pour l'émetteur que pour le récepteur est difficile.**

II / Les stratégies anti-prédatrices et la communication

1) Les différentes stratégies anti-prédatrices

Darwin (1859) fut le premier à suggérer que la sélection exercée par la prédation est à l'origine de l'apparition de stratégies anti-prédatrices permettant aux proies d'augmenter leur chance d'échapper à la prédation. Ces stratégies anti-prédatrices reposent sur des adaptations qui peuvent être comportementales, morphologiques, ou physiologiques (Lima & Dill 1990, Tollrian & Harvell 1999, Creel & Christianson 2008). Les adaptations morphologiques pour faire fuir le prédateur et physiologiques comme la sécrétion d'hormones de stress permettant à l'animal une réaction rapide, ou le mimétisme qui minimise les chances d'être détecté sont courantes et ont donné lieu à de nombreuses publications. Concernant les réponses comportementales, on retrouve chez de nombreuses espèces d'oiseaux et de mammifères les cris d'alarmes émis lorsqu'un prédateur se trouve à proximité ou attaque (Klump & Shalter 1984, Manser 2001, Graw & Manser 2007, Krams et al. 2008).

Les cris d'alarme sont classés selon le degré ou le type de menace, la réponse déclenchée, l'état présumé, l'intention de l'émetteur ou la structure acoustique (Tableau 1). La nature des cris d'alarme (structure temporelle et spectrale) varie en fonction des espèces et de la situation (Tableau 1) mais de nombreuses espèces produisent trois types de cris d'alarme (Magrath et al. 2015a): (*i*) les cris d'alarme de fuite (*Flee alarm call*) souvent émis pour un prédateur qui représente un danger immédiat (e.g. les prédateurs mobiles, les rapaces en vol notamment). Ces cris provoquent la fuite des proies potentielles; (*ii*) les cris de harcèlement (*Mobbing alarm call*) produits pour un prédateur qui n'évoque pas un danger immédiat (e.g. prédateurs terrestres ou aux rapaces perchés) mais pourrait le devenir s'il restait dans la zone (Caro 2005). Ils permettent de recruter les autres proies potentielles pour harceler le prédateur (Hartley 1950); et (*iii*) les cris de détresse (*Distress call*), émis lorsqu'un individu est attaqué ou capturé, ce qui pourrait surprendre le prédateur ou permettre de recruter d'autres individus pour aider l'émetteur (Schmidt & Johnson 1983). Il y a eu relativement peu d'études sur les cris de harcèlement contrairement aux cris de détresse et de fuite. Dans la mesure où ces phénomènes ne se manifestent qu'en présence de prédateur, il est admis qu'il s'agit bien de stratégies anti-prédatrices (Harvey & Greenwood 1978, Reudink et al. 2007, Sandoval & Wilson 2012).

Tableau 1 : Liste et définition des différentes types de cris d'alarme (d'après Magrath et al. 2015a).

Terme	Contexte de production/definition	Réponse typique des récepteurs	Autre utilité
Cris d'alarme de fuite (*Flee alarm call*)	Cri induit par un prédateur en chasse, posant souvent un danger immédiat. Les cris émis pour les rapaces en vol sont souvent appelés "cris d'alarme aériens".	Les proies deviennent cryptiques, fuient pour se cacher ou deviennent vigilantes (parfois en regardant vers le haut les cris aériens).	Parfois appelés "cris d'avertissement ". Peut être nommé d'après le type de menace (comme l'alarme "faucon" ou "aigle"), ou des caractéristiques acoustiques (comme le cris d'alarme "seet" de certaines espèces).
Cris de harcèlement (*Mobbing call*)	Cri lancé envers un prédateur perché ou un prédateur terrestre qui ne constitue pas une menace immédiate. Potentiellement dirigé vers d'autres proies ou vers le prédateur.	Les proies s'approchent de l'appelant, émetent des cris de harcèlement et harcèlent le prédateur. Les prédateurs sont chassés par les proies. Les individus vulnérables, comme les jeunes, peuvent devenir silencieux ou cryptiques plutôt que de s'approcher.	Peut être appelé alarme "assemblage", alarme "terrestre", ou nommé telle que alarme "léopard" ou "serpent". Les cris qui sont dirigés vers un prédateur peuvent être appelés "cris de défense".
Cris de détresse (*Distress call*)	Cri déclenché lorsqu'un individu est coincé, attaqué ou capturé.	Les proies peuvent s'approcher. Le prédateur attaquant peut être surpris ou trompé; d'autres prédateurs peuvent s'approcher.	Peut être nommé d'après les propriétés acoustiques, comme le sifflement ou le cliquetis. Également appelés "signaux de la victime" ; certains peuvent agir comme des "cris de distraction". Les cris qui menacent un prédateur peuvent être appelés "appels à la défense".
Cri d'alarme progressif (*Graded alarm call*)	Cri qui varie quantitativement en fonction de certaines propriétés du prédateur, comme sa proximité. Peut donc indiquer l'urgence ou le degré de risque.	Les proies modifient la réponse en fonction des caractéristiques quantitatives de l'appel. Les réponses comprennent une action plus immédiate pour les cris codant une urgence plus grande.	Lorsqu'il s'agit du degré de danger, on parle d'un cri d'alarme "lié à l'urgence" ou "basé sur le risque".
Cris d'alarme référentiel (*Referential alarm call*)	Cri émis envers un prédateur ou une menace spécifique.	Les proies réagissent de manière appropriée pour éviter ce type de prédateur ou de menace.	Également appelés cris d'alarme "fonctionnellement référentiels " ou "spécifiques aux prédateurs", ou nomme des prédateurs spécifiques, tels que les alarmes " aigle ", "léopard " et " serpent ".
Cris d'alerte (*Alert call*)	Cri déclenché par la présence d'un prédateur ou d'autres menaces ou perturbations.	Les conspécifiques deviennent attentifs et réagissent différemment selon le contexte.	Peut être appelé "cri d'alarme générale", car ils sont émis dans une large gamme de menaces ou de perturbations.

2) Le cas particulier du comportement de harcèlement

a) Description

Parmi les stratégies anti-prédatrices mises en place chez les animaux, le comportement de harcèlement du prédateur (*mobbing*) est un comportement surprenant puisqu'il consiste non pas à fuir comme le font la plupart des proies mais à aller vers le prédateur pour provoquer son départ (Hartley 1950, Curio 1978, Caro 2005, Campbell & Snowdon 2007, Carlson et al. 2018). Cette stratégie est fréquente chez les oiseaux (Altmann 1956, Curio 1978, Desrochers et al. 2002, Krams & Krama 2002, Maklakov 2002, Templeton et al. 2005) et également présente au sein d'autres taxons comme les mammifères (Owings & Coss 1977, Tamura 1989, Colquhoun 2006, Graw et Manser 2007, Knörnschild & Tschapka 2012), les poissons (Dominey 1983, Helfman 1989, Dugatkin & Godin 1992) et les insectes (Seeley et al. 1982, Kastberger et al. 2014). La majorité des études a montré que les cibles du harcèlement sont les serpents et les rapaces (e.g. Tamura 1989, Maklakov 2002, Graw & Manser 2007, Crofoot 2012, Cunha et al. 2017).

D'un point de vue mécanistique, le comportement de harcèlement peut se décrire de la façon suivante (Altmann 1956, Zimmermann & Curio 1988) : détection du danger par l'émetteur, émission d'un signal de harcèlement avec approche et harcèlement du prédateur (Figure 2). L'émission du signal qui s'accompagne d'un rapprochement du prédateur permet de recruter d'autres proies potentielles congénères et hétérospécifiques pour participer au harcèlement du prédateur (Marler 1957, Zimmermann & Curio 1988, Hurd 1996, Templeton & Greene 2007). L'information véhiculée étant publique, celle-ci peut donc être utilisée par différents acteurs (Ito & Mori 2009, Templeton & Greene 2007). **Un des objectifs de cette thèse a été de quantifier la variabilité de réponse aux signaux intraspécifiques et interspécifiques et d'explorer les sources de cette variabilité.**

Le harcèlement permettrait de décourager le prédateur (Sherman 1977, Gursky 2006). Plusieurs études ont montré que le comportement de harcèlement va jusqu'à faire partir le prédateur (*move-on hypothesis*, Curio 1978, Pettifor 1990, Flasskamp 1994, Gursky 2006, Krams et al. 2009). A l'appui de cette hypothèse, des études suggèrent que les cris de harcèlement peuvent « stresser » les prédateurs (Shalter 1978, Flasskamp 1994, Consla & Mummen 2012). Cela peut même conduire à modifier l'abondance locale des prédateurs. Par exemple, Pavey et Smyth (1998) suggère que la chouette d'Australie (*Ninox strenua*) se retrouve plus souvent dans les forêts tropicales que dans les forêts ouvertes car le harcèlement y est possiblement moins fréquent. Concernant les risques associés à cette stratégie, l'émetteur se signale au prédateur ce qui probablement augmente le risque qu'il se fasse capturer. Certains travaux ont permis de montrer que les animaux harceleurs peuvent se faire capturer par le prédateur (Denson 1979, Curio & Regelmann 1986, Montgomerie & Weatherhead 1988, Poiani & Yorke 1989, Motta-Junior 2007). Les signaux de harcèlement peuvent orienter le prédateur (Krams 2001) et peuvent être coûteux car ils sont localisables et indiqueraient la position des proies à des prédateurs potentiels. Deux études expérimentales (Krama & Krams 2004, Krams et al. 2007) ont permis de révéler que les cris de harcèlement de gobemouche noir (*Ficedula hypoleuca*) augmentent la prédation du nid. Il existe probablement d'autres coûts énergétiques associés à ces comportements (Dugatkin & Godin 1992), mais ceux-ci restent probablement faibles par rapport au budget énergétique journalier ou par rapport au coût énergétique de l'effort de vigilance.

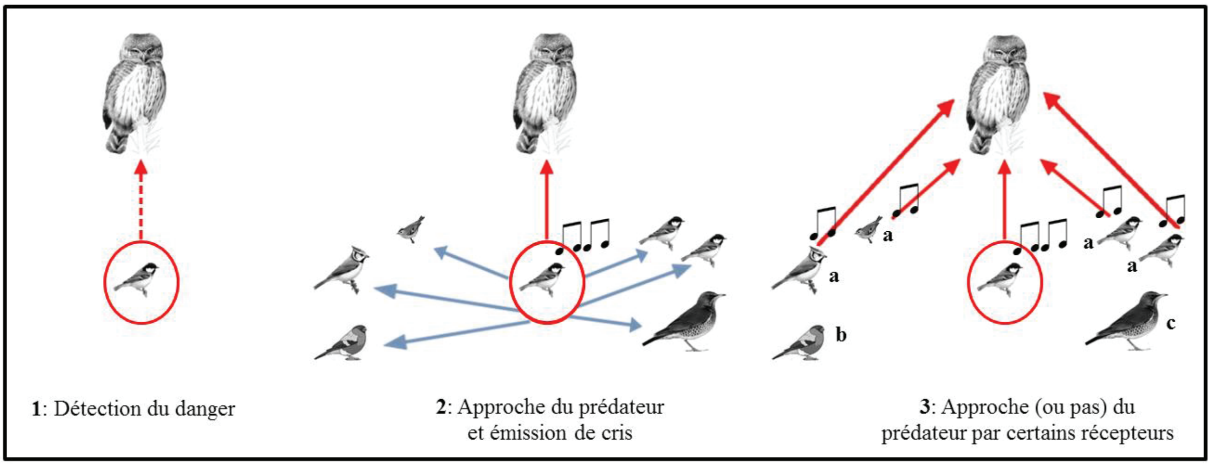

Figure 2 : Schéma expliquant la séquence comportementale du harcèlement. Un individu détecte un danger (1), puis approche et harcèle le prédateur en émettant un signal de harcèlement destiné aux conspécifiques et hétérospécifiques (2). En bout de chaine (3) : différentes réactions selon l'espèce liées au risque de prédation : (a) certains individus changent de comportement, s'approchent et harcèlent le prédateur en émettant aussi des cris de harcèlement permettant de recruter d'autres proies ; (b) certains individus changent de comportement mais ne s'approchent pas du prédateur, ils peuvent être classés de « tricheurs » ; (c) certains individus ne changent pas de comportement et ne s'approchent pas du prédateur. Dans ce dernier cas, le cris de harcèlement est perçu comme un bruit et ne porte pas d'information importante à prendre en compte.

Les chances de détection du prédateur et de succès du harcèlement sont d'autant plus grandes que le nombre de participants est important (Pulliam 1973, Becker 1984, Robinson 1985, Verbeek 1985, Cresswell 1994) favorisant ainsi de la communication interspécifique (Klump Shalter 1984, Caro 2005). Un nombre élevé d'individus harcelant un prédateur permet une diminution du risque d'être tué (*Safety in numbers hypothesis*, Hamilton 1971, Hogan et al. 2017) en réduisant la probabilité d'une attaque réussie d'un prédateur en raison de l'effet de confusion (Miller 1922, Cunha et al. 2017). Les cris spécifiques possèdent des caractéristiques qui améliorent la localisation de l'émetteur permettant de recruter un plus grand nombre d'individus contre le prédateur (Marler 1955).

Plusieurs travaux ont montré que les proies ne harcèlent pas des espèces non prédatrices (mais voir Graw & Manser 2007, Crofoot 2012) mais uniquement leur prédateur (Kobayashi 1987, Lind et al. 2005, Griesser 2009). Le comportement de harcèlement est donc typique d'un prédateur et les proies sont capables de distinguer une espèce prédatrice d'une espèce non prédatrice (Kobayashi 1987, Lind et al. 2005, Krams et al. 2007). Toutefois, la plupart des études a jusqu'à ce jour opposé l'espèce prédatrice ciblée à des espèces inoffensives ou a été conduite sur une espèce spécifique et non pas à l'échelle de la communauté (mais voir Cuhna et al. 2017). Par ailleurs, le harcèlement varie selon la saison et une association entre saison de reproduction et intensité du harcèlement a été rapportée chez un grand nombre d'espèces (Altmann 1956, Shedd 1982, Swaisgood et al. 1999, Krams et al. 2007). **Un objectif supplémentaire de cette thèse a été de savoir comment le risque de prédation et la saison modulent le comportement de harcèlement.**

b) Causes ultimes impliquées dans l'expression du comportement de harcèlement

Pour apprécier le comportement de harcèlement dans son ensemble, il faut tout d'abord comprendre pourquoi les individus se mobilisent autour du prédateur. Bien qu'un certain nombre de théories sur la manière et les raisons pour lesquelles le harcèlement a évolué ait été proposé, deux mécanismes majeurs ont été identifiés: l'intérêt propre ou l'altruisme réciproque (Curio 1978).

Les motivations fondées sur l'intérêt propre peuvent être soit directes soit indirectes (*kin selection*). Les avantages directs pour les individus harcelant un prédateur incluent : la chasse du prédateur hors d'une zone (Pettifor 1990, Flasskamp 1994), alerter le prédateur de sa découverte, décourageant ainsi l'attaque (Flasskamp 1994) et la réduction de la pression de prédation locale (Ekman 1986, Pavey & Smyth 1998). Les bénéfices indirects pour les individus harcelant un prédateur se manifestent lorsqu'un individu est altruiste envers ses proches (*kin*), augmentant ainsi indirectement sa *fitness* (Consla & Mumme 2012, Knight & Temple 1986). Cela implique que les émetteurs peuvent augmenter leur valeur adaptative en avertissant régulièrement leurs proches. Cette hypothèse est basée sur la sélection de parentèle proposée par Hamilton (1963). Les cris de harcèlement ont donc probablement évolué à travers la sélection de parentèle dans la façon dont, en protégeant leur progéniture, les individus qui alarment protègent leurs propres gènes. En effet, de nombreuses espèces sont plus susceptibles de harceler et de produire des cris de harcèlement lorsque des membres de la famille sont présents (e.g. cardinal rouge, *Cardinalis cardinalis*, Gehlbach & Leverett 1995; mésangeai imitateur *Perisoreus infaustus*, Griesser 2009, écureuil à ventre rouge, *Callosciurus erythraeus thaiwanensis*, Tamura 1989). Bien qu'il existe des exemples où seuls les apparentés sont les bénéficiaires, un certain nombre d'espèces se livre au harcèlement en présence d'individus non apparentés (Barash 1974), ce qui indique que la *kin-selection* n'explique que certains comportements de harcèlement.

Dans le cas général et surtout chez les oiseaux, la stratégie de harcèlement fait souvent intervenir plusieurs espèces et cela exclue probablement l'hypothèse de sélection de parentèle comme mécanisme évolutif impliqué dans le maintien de la stratégie de harcèlement. Le succès du harcèlement dépend du nombre de participants et du contexte social (Robinson 1985, Krams et al. 2006). Par conséquent, la réciprocité entre individus voisins doit être importante pour réussir à harceler un prédateur (Kruuk 1964, Slagsvold 1980). Le premier individu qui harcèle augmente son risque de prédation en attirant l'attention du prédateur (Krams 2001). Si les voisins coopèrent au harcèlement, les harceleurs ont effectivement une chance accrue de conduire le prédateur en dehors de la zone de reproduction (Pettifor 1990, Flasskamp 1994). Si aucun voisin ne coopère avec le premier individu qui harcèle, le harceleur solitaire prend un risque mortel (Hoogland & Sherman 1976, Denson 1979, Curio & Regelmann 1985, Poiani & Yorke 1989). Plusieurs études indiquent que l'origine du harcèlement est due à la coopération réciproque. Les résultats de Krams et de ses collègues (2006, 2008, 2009) montrent que l'origine et l'évolution du comportement de harcèlement du gobemouche noir peuvent être expliquées en termes d'altruisme réciproque. Les individus coopèrent pour harceler le prédateur des nids des voisins, mais aident seulement les voisins qui les ont aidés dans le passé. Une étude réalisée sur le pinson des arbres (*Fringilla coelebs*, Krams & Krama 2002) indique que la coopération entre les individus appartenant à des espèces différentes pour faire partir le prédateur peut être expliquée comme la réciprocité interspécifique fondée sur la reconnaissance interspécifique et la stabilité temporelle des communautés de reproduction. Les auteurs indiquent que le pinson peut s'engager dans une coopération mutuelle avec des voisins si les oiseaux ont une probabilité minimum de se revoir. Les auteurs pensent que les individus dans toutes les communautés d'oiseaux sédentaires coopèrent dès qu'ils ont établi leurs territoires. Dans ce cas, l'altruisme réciproque peut être utilisé pour expliquer la mise en place et le maintien de la stratégie de harcèlement.

Une des façons de communiquer efficacement entre les espèces différentes réside dans le fait d'utiliser des signaux identiques chez toutes les espèces. La forme simple de certains cris (bien que de récentes études aient mis en évidence des systèmes de codage/décodage complexes permettant de transférer des informations; voir partie II.2.c. ci-dessous) et leur possibilité d'être localisables probablement liée à la largeur de bande de fréquence pour le récepteur pourrait être à l'origine de phénomène de convergence responsable de leur valeur interspécifique. Marler (1955) suggère que le support fonctionnel du signal (i.e. le type d'émission sonore) devrait conduire à une convergence des caractéristiques acoustiques chez les différents taxa. Afin de mettre en évidence un phénomène de convergence au sein d'un type de vocalisation, il est nécessaire de le comparer à un autre type de vocalisation (i.e. étudier au moins deux supports fonctionnels). A notre connaissance, parmi les études qui se sont penchées sur l'évolution des cris de harcèlement entre les différentes espèces d'oiseaux (Latimer 1977, Ficken & Popp 1996, Proppe at al. 2010, Wheatcroft & Price 2014, Billings 2018), de telles comparaisons n'ont pas été réalisées (mais voir Latimer 1977 et Wheatcroft & Price 2014). **Un objectif supplémentaire de cette thèse a été de savoir si la convergence des structures des cris de harcèlement existe chez les oiseaux**.

c) Les cris de harcèlement : comment coder de l'information ?

Chez certaines espèces, les cris de harcèlement sont complexes et transmettent aux conspécifiques et hétérospécifiques des informations précises sur le prédateur (Templeton et al. 2005, Templeton & Greene 2007, Hetrick & Sieving 2011, Dahl & Ritchison 2018). Cette complexité est liée au nombre et au type de notes qui composent le signal. Les cris de harcèlement sont bien décrits chez les Paridés (Lucas & Freeberg 2007, Hetrick & Sieving 2011, Suzuki et al. 2016, Carlson et al. 2017a) et sont généralement composés d'une combinaison d'éléments modulés en fréquence (*frequency modulated elements*: FME) suivis par un enchainement d'éléments à large bande de fréquence appelés notes D facilement localisables. Les signaux transmis par l'émetteur sont modulés en fonction du danger perçu (Graw & Manser 2007) et peuvent contenir des informations précises sur le prédateur (Templeton et al. 2005, Hetrick & Sieving 2011). Par exemple, les cris de harcèlement émis par la mésange à tête noire (*Poecile atricapillus*) codent des informations sur la taille ou le risque représenté par un prédateur (Templeton et al. 2005; Figure 3).

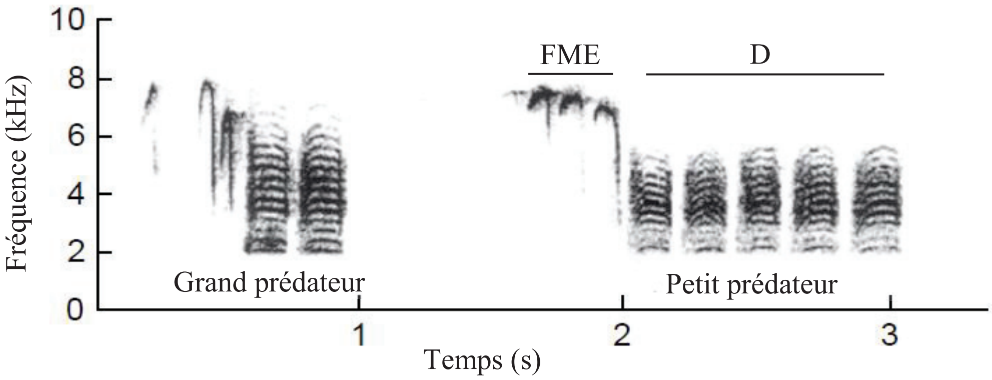

Figure 3 : Cris de harcèlement émis par la mésange à tête noire (*Poecile atricapillus*) codant des informations sur la taille et le risque des prédateurs. FME : *frequency modulated elements* suivis par un enchainement d'éléments à large bande de fréquence appelés notes D facilement localisables.

Comme l'ont suggéré plusieurs auteurs, le patron FME-D pourrait bien découler d'une organisation hiérarchisée suivant une règle syntaxique (Hailman & Ficken 1986, Lucas & Freeberg 2007). Plus particulièrement, trois récentes études (Engesser et al. 2016, Suzuki et al. 2016, Suzuki et al. 2017) affirment avoir montré que les passereaux - la mésange de Chine (*Parus minor*) et le cratérope bicolore (*Turdoides bicolor*) - combinent syntaxiquement des unités acoustiques pour créer un cri possédant des significations plus complexes, à savoir le cri de harcèlement. Dans d'autres termes, les auteurs suggèrent que ces animaux possèdent un système de codage de l'information similaire au langage humain : la syntaxe compositionnelle. Dès lors que les cris de harcèlement ont la particularité de rameuter un grand nombre d'hétérospécifiques, ceux-ci pourraient utiliser la syntaxe afin de décoder des informations mais cela reste pour le moment une énigme. Ainsi, les cris de harcèlement constituent un type de signal particulièrement intéressant pour l'étude de la syntaxe chez les animaux. **Au cours de cette thèse j'ai donc cherché à savoir si l'utilisation de la syntaxe pour coder et/ou extraire des informations dans les cris de harcèlement existe chez d'autres espèces de passereaux.**

d) Ontogénèse du comportement de harcèlement

L'utilisation de signaux hétérospécifiques peut, soit résulter d'un apprentissage que seule l'expérimentation permet de mettre en évidence, soit/et être le résultat d'une similitude de structures acoustiques (Magrath et al. 2015a). Une réponse non apprise peut permettre aux individus de répondre à des signaux sans expérience au préalable, par exemple à la sortie du nid, minimisant ainsi l'exposition aux prédateurs (Hollén & Radford 2009). Au contraire, si l'apprentissage peut permettre une certaine flexibilité, il présente un inconvénient important : les individus ont besoin d'expériences avant de pouvoir agir de manière appropriée (Griffin

2004). Malgré un nombre d'études croissant sur les réponses hétérospécifiques, les mécanismes impliqués dans la reconnaissance des signaux hétérospécifiques de harcèlement sont encore mal compris (Magrath et al. 2015a).

Tout d'abord, les individus pourraient apprendre à répondre aux signaux interspécifiques par association directes entre la présence des prédateurs et des signaux d'alarme interspécifiques. L'apprentissage par l'expérience directe peut être avantageux parce qu'il évite les erreurs en copiant le comportement des autres et il est relativement facile de faire des associations directes entre les prédateurs et d'autres signaux liés au danger (Hurd 1996). Apprendre à reconnaître des appels d'alarme hétérospécifiques à partir de l'expérience personnelle peut être risqué si cela implique une exposition aux prédateurs. En raison de ces faibles risques associés au harcèlement, l'apprentissage direct peut être plus commun dans cette situation par rapport à une situation où le risque est élevé (Caro 2005). Les signaux acoustiques et visuels émis durant un épisode de harcèlement donnent au jeune animal naïf des indications concernant ceux dont il doit se méfier et comment harceler à son tour. Chez les suricates, l'intensité du harcèlement est corrélée à l'âge de l'individu (Graw & Manser 2007). Les jeunes apprennent à harceler les prédateurs en observant les adultes et le comportement de harcèlement de chaque individu change avec l'expérience. Il a aussi été montré que le merle noir (*Turdus merula*) apprend à harceler un prédateur (*Philemon corniculatus*) auquel il était initialement indifférent après avoir vu un conspécifique l'assaillir (Curio et al. 1978). Finalement, un processus de généralisation des réponses apprises pourrait également être un mécanisme permettant de répondre à de nouveaux cris d'alarme (Ghirlanda & Enquist 2003, ten Cate & Rowe 2007, Getschow et al. 2013). Une telle généralisation pourrait provenir des réponses apprises à partir de cris conspécifiques ou hétérospécifiques. En effet, l'apprentissage de ces cris suivi d'un processus de généralisation permettrait la réponse aux signaux inconnus mais acoustiquement similaires (Weary 1991, Ghirlanda & Enquist, 2003, Sturdy et al. 2007).

Que ce soit dû au hasard, à la conservation phylogénétique ou à la sélection, les similitudes acoustiques retrouvées dans les cris de différentes espèces peuvent permettent des réponses sans apprentissage (Marler 1955, Randler 2012). Randler en 2012 suggère que la réponse hétérospécifique est conservée dans la phylogénie et montre qu'un mécanisme de reconnaissance est conservé dans la famille Paridae. Le degré de menace posé par le prédateur est codé dans les cris de harcèlement est perçu par tous les Paridae, capables de répondre à ces cris. Cependant, il a été mis en évidence que certaines espèces ne répondent pas aux cris de harcèlement allopatriques (Nocera et al. 2008).

Tous ces résultats indiquent que différents mécanismes sont impliqués dans la reconnaissance des signaux de harcèlement, et implique de connaître la part relative liée à chaque mécanisme.

III / Objectifs et hypothèses

L'objectif de cette thèse est de comprendre comment une réponse au prédateur se met en place et quelles sont les règles de la communication intraspécifique et interspécifique dans le cas du comportement de harcèlement (Figure 4). J'ai travaillé sur l'évolution de la signalisation et le transfert d'informations entre plusieurs espèces de passereaux.

Dans un premier temps, nous avons étudié les facteurs proximaux déterminant la mise en œuvre du comportement de harcèlement au sein d'une communauté de proies, et tout particulièrement les variations du risque de prédation pouvant résulter de la biologie des proies et des caractéristiques du prédateur. Dans un second temps, nous avons quantifié la variabilité de réponse aux signaux acoustiques intra et interspécifiques. Dans un troisième temps, afin de comprendre quels facteurs expliquent la variabilité de la réponse des passereaux aux signaux acoustiques, nous avons évalué le poids de la proximité structurale des signaux et testé l'existence d'une convergence en tenant compte de la proximité phylogénétique des espèces. Nous avons également déterminé si la syntaxe compositionnelle pouvait être un système de codage/décodage de l'information entre les espèces. Enfin, nous avons étudié le rôle de l'apprentissage dans la réponse aux signaux de harcèlement.

Les différentes hypothèses éprouvées au cours de cette thèse balayent ces différents aspects :

- Hypothèse 1 : le comportement de harcèlement varie en fonction du risque de prédation et implique de la communication interspécifique (*Articles 1 et 2*)
- Hypothèse 2 : les animaux répondent plus aux signaux intraspécifiques qu'aux signaux hétérospécifiques (*Article 4*)

- Hypothèse 3 : les animaux répondent aux cris de harcèlement en fonction de leur similitude structurale avec leurs propres cris de harcèlement (*Article 4*)

- Hypothèse 4 : la saison a un effet sur le comportement de harcèlement (*Articles 2 et 3*)

- Hypothèse 5 : les signaux de harcèlement des différentes espèces sont plus similaires entre eux que les chants territoriaux de ces espèces (*Articles 5*)

- Hypothèse 6 : les mésanges utilisent la syntaxe compositionnelle pour coder/extraire des informations dans leurs cris de harcèlement (*Article 6*)

- Hypothèse 7.a. : la réponse envers des cris de harcèlement d'espèces inconnues ne requière pas d'apprentissage chez les adultes (*Article 4*)

- Hypothèse 7.b : les jeunes sont capables d'associer un signal neutre à des cris de harcèlement (*Article 7*).

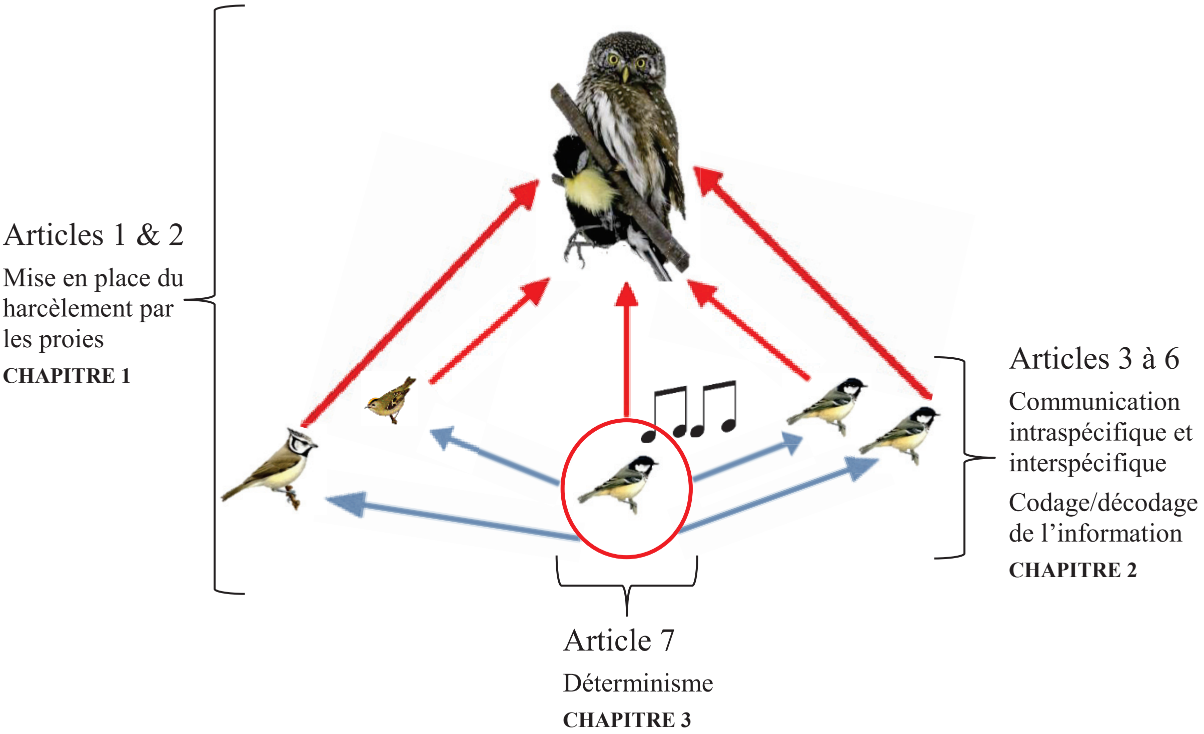

Figure 4 : Objectifs de travail de cette thèse exposés en 7 articles. L'émetteur du signal (entouré en rouge) émet des cris de harcèlement envers les conspécifiques (à droite) et les hétérospécifiques (à gauche) qui vont aller harceler le prédateur (chevêchette). J'ai essayé de comprendre ce système dans sa globalité, en partant des facteurs proximaux qui vont déterminer la mise en place du comportement de harcèlement (articles 1 et 2), en passant par les facteurs expliquant les réponses intraspécifiques et interspécifiques (articles 3 à 6), la part liée à l'apprentissage (article 7) jusqu'aux systèmes de codage/décodage de l'information (article 6) au sein d'une communauté de proies.

IV / Modèles biologiques

1) 1 espèce de prédateur et 36 espèces de passereaux étudiées…

Afin d'étudier la réponse à un prédateur spécifique, une communauté de passereaux européens regroupant 22 espèces a été exposée à la chevêchette d'Europe (*Glaucidium passerinum*), une petite chouette de montagne connue pour consommer des oiseaux (Solheim 1984, Henrioux 2013, 2014, Muller & Riols 2013). La variation d'exposition au risque de prédation imposée aux passereaux par cette espèce de chouette est la base de la diversité des réponses attendues chez les passereaux. La variation de réponse aux cris de harcèlement intraspécifiques et interspécifiques a ensuite été quantifiée chez 4 espèces de passereaux européens. Pour deux d'entre elles, la mésange bleue (*Cyanistes caeruleus*) et la mésange charbonnière (*Parus major*), des tests ont été réalisés au printemps et à l'automne dans le but de tester l'effet de la saison. Afin d'étudier la part liée à l'apprentissage, j'ai d'une part testé quatre espèces européennes avec des signaux inconnus émis par trois espèces nord-américaines. D'autre part, j'ai cherché à déterminer si les poussins de mésange charbonnière étaient capables d'associer un signal acoustique neutre avec des cris de harcèlement. Une analyse de la structure des cris de harcèlement de 23 espèces appartenant à 9 familles a également été réalisée afin d'évaluer la similitude et la divergence/convergence des structures acoustiques entre les espèces (voir Figure 5 pour un exemple de sonagramme). Enfin, j'ai étudié le système de codage de l'information dans les cris de harcèlement chez la mésange charbonnière et testé ce système à échelle intraspécifique et interspécifique (mésange noire *Parus ater* et pinson des arbres *Fringilla coelebs*). Une liste des 36 espèces de passereaux étudiées (sans compter la chevêchette) est fournie dans le tableau 2 ci-dessous.

Les espèces européennes sur lesquelles nous avons réalisé des tests bénéficient d'une protection totale sur le territoire français depuis l'arrêté ministériel du 17 avril 1981 relatif aux oiseaux protégés sur l'ensemble du territoire. Elles sont protégées et font partie de l'Annexe III – Espèces de faune protégées de la Convention relative à la conservation de la vie sauvage et du milieu naturel de l'Europe traité n° 104 Berne, 19/09/1979.

2) …et une attention particulière pour la mésange charbonnière

La mésange charbonnière a été l'espèce sur laquelle j'ai le plus travaillé. Elle a été choisie comme modèle biologique dans tous les articles. Le paragraphe qui suit n'a nullement la prétention de décrire l'écologie de cette espèce; en revanche, il présente le comportement de harcèlement, le système de communication et les vocalises mis en place par la mésange.

La mésange charbonnière est l'espèce du genre *Parus* la plus largement répandue. Elle est présente partout en Europe, en Afrique du Nord et dans la majeure partie de l'Asie. Ce passereau est reconnu pour ses performances cognitives et capacités d'apprentissage (Exnerova et al. 2011, Morand-Ferron 2015). Monogame et nichant dans des cavités, cette espèce accepte facilement de se reproduire dans des nichoirs artificiels, ce qui en facilite le suivi lors de la reproduction (Gosler 1993). Peu farouche et commune en France, la mésange est un modèle de choix pour des tests comportementaux en captivité, car elle s'habitue facilement aux conditions expérimentales (Cole et al. 2011) et en milieu naturel où elle est facile à capturer et à identifier. En dehors de la saison de reproduction, les mésanges charbonnières occupent de grands regroupements multi-spécifiques (Hinde 1952). La mésange charbonnière est connue pour harceler les prédateurs de passereaux comme la chevêchette perlée (*Glaucidium perlatum*), la chevêchette d'Europe ou encore l'épervier d'Europe (*Accipiter nisus*) (Regelmann & Curio 1983, Lind et al. 2005, Carlson et al. 2017b, Carlson et al. 2017c). Lorsqu'elle harcèle, elle émet des cris composés de plusieurs éléments ayant des caractéristiques qui améliorent la localisation de l'émetteur (i.e. large bande de fréquence) (Klump & Shalter 1984, Carlson et al. 2017a). Cette espèce serait capable de coder des informations comme la dangerosité du prédateur dans ses cris (Carlson et al. 2017a). Les récentes études menées au Japon sur une espèce phylogénétiquement proche (*P. minor*) avec laquelle elle peut s'hybrider (Paeckert et al. 2005, Kvist & Rytkoenen 2006, Johansson et al. 2013) indiquent que la mésange de Chine produit des cris de harcèlement différents selon le prédateur rencontré. Elle émet des cris nommés « jar » envers les serpents et des cris nommés « chicka » pour les autres prédateurs comme les corbeaux à gros bec (*Corvus macrorhynchos*) ou encore les martres (Suzuki 2011, 2014). Ces cris, composés de quatre notes (nommées A, B, C et D) composants des mots basés sur des règles combinatoires (Suzuki et al. 2016, 2017), transmettent des informations sur le type de prédateur de nid (serpents *versus* prédateurs non-serpents) aux parents (Suzuki 2012) et aux oisillons (Suzuki 2011).

La mésange charbonnière est donc un modèle biologique pertinent permettant de mesurer les effets de la prédation sur l'évolution du comportement de harcèlement et de la communication d'un point de vue comportemental.

Tableau 2 : Liste des 36 espèces de passereaux étudiées pour leurs cris de harcèlement et/ou testées lors des tests de repasse présentées dans l'ordre alphabétique.

Nom commun	**Nom Latin**	**Origine (contient/pays)**	Article 1	Article 2	Article 3	Article 4	Article 5	Article 6	Article 7
			repasse	repasse	repasse + analyse acoustique	repasse	repasse	analyse acoustique	repasse
Bec-croisé des sapins	*Loxia curvirostra*	Europe		✓					
Bouvreuil pivoine	*Pyrrhula pyrrhula*	Europe		✓					
Cassenoix moucheté	*Nucifraga caryocatactes*	Europe		✓					
Geai des chênes	*Garrulus glandarius*	Europe		✓					
Gobemouche noir	*Ficedula hypoleuca*	Europe						✓	
Grimpereau des bois	*Certhia familiaris*	Europe		✓					
Grimpereau des jardins	*Certhia brachydactyla*	Europe		✓					
Grive draine	*Turdus viscivorus*	Europe		✓					
Grive musicienne	*Turdus philomelos*	Europe		✓					
Gros-bec casse-noyaux	*Coccothraustes coccothraustes*	Europe		✓					
Merle noir	*Turdus merula*	Europe		✓					
Méliphage bruyant	*Morina melanocephala*	Australie						✓	
Mésange à longue queue	*Aegithalos caudatus*	Europe		✓					
Mésange à tête noire	*Poecile atricapillus*	Amérique du Nord			✓			✓	
Mésange bleue	*Cyanistes caeruleus*	Europe	✓	✓	✓	✓		✓	
Mésange bicolore	*Baeolophus bicolor*	Amérique du Nord			✓			✓	
Mésange boréale	*Poecile montanus*	Europe		✓				✓	
Mésange charbonnière	*Parus major*	Europe	✓	✓	✓	✓	✓	✓	✓
Mésange de Chine	*Parus minor*	Chine/Japon						✓	
Mésange huppée	*Lophophanes cristatus*	Europe	✓	✓				✓	
Mésange noire	*Periparus ater*	Europe	✓	✓	✓		✓	✓	
Paruline couronnée	*Seiurus aurocapilla*	Amérique du Nord						✓	
Paruline jaune	*Setophaga petechia*	Amérique						✓	
Paruline du Canada	*Cardellina canadensis*	Amérique						✓	
Pinson des arbres	*Fringilla coelebs*	Europe	✓	✓	✓		✓	✓	
Roitelet huppé	*Regulus regulus*	Europe	✓	✓					
Roitelet triple-bandeau	*Regulus ignicapilla*	Europe	✓	✓					
Rougegorge familier	*Erithacus rubecula*	Europe	✓	✓				✓	
Sittelle à poitrine blanche	*Sitta carolinensis*	Amérique du Nord						✓	
Sittelle à poitrine rousse	*Sitta canadensis*	Amérique du Nord						✓	
Sittelle torchepot	*Sitta europaea*	Europe		✓				✓	
Sporophile à col blanc	*Sporophila torqueola*	Amérique du Nord						✓	
Troglodyte de Caroline	*Thryothorus ludovicianus*	Amérique du Nord			✓			✓	
Troglodyte mignon	*Troglodytes troglodytes*	Europe		✓				✓	
Viréo à oeil rouge	*Vireo olivaceus*	Amérique						✓	
Viréo à tête bleue	*Vireo solitarius*	Amérique du Nord						✓	

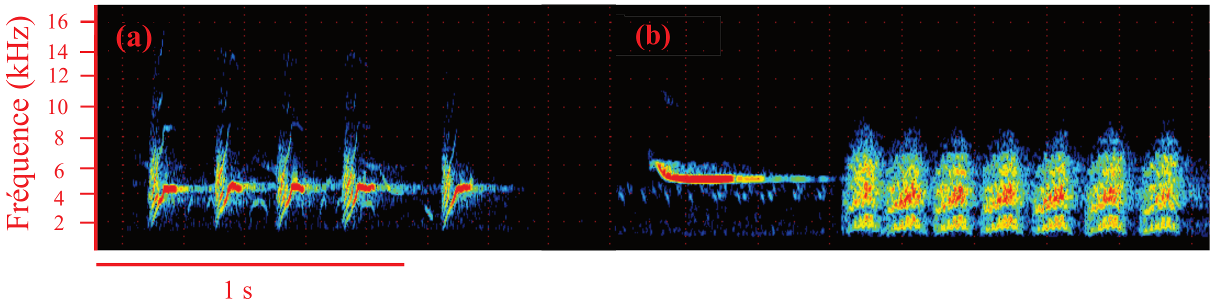

Figure 5 : Sonagramme de cris de harcèlement permettant de visualiser l'intensité énergétique du cri selon un gradient de couleur (couleurs froides = intensités faibles, couleurs chaudes = intensités fortes) du pinson des arbres *Fringilla coelebs* (a) et de la mésange charbonnière *Parus major* (a)).

Présentation des articles

Chapitre 1 : Harcèlement des prédateurs : comment expliquer la mise en place d'une telle stratégie par les proies ?

[1] **Dutour, M.**, Léna, J.P., & Lengagne, T. (2016). Mobbing behaviour varies according to predator dangerousness and occurrence. *Animal Behaviour*, *119*, 119-124. doi : 10.1016/j.anbehav.2016.06.024

[2] **Dutour, M.**, Léna, J.P., & Lengagne, T. (2017). Mobbing behaviour in a passerine community increases with prevalence in predator diet. *Ibis*, *159*, 324-330. doi : 10.1111/ibi.12461

Chapitre 2 : Appeler au harcèlement : une communication tournée à la fois vers les conspécifiques et les hétérospécifiques

[3] **Dutour, M.**, Cordonnier, M., Léna, J. P., & Lengagne, T. (2018). Seasonal variation in mobbing behaviour of passerine birds. *Journal of Ornithology, resoumis août 2018*

[4] **Dutour, M.**, Léna, J. P., & Lengagne, T. (2017). Mobbing calls: a signal transcending species boundaries. *Animal Behaviour*, *131*, 3-11. doi : 10.1016/j.anbehav.2017.07.004

[5] **Dutour, M.**, Lengagne, T., & Léna, J. P. (2018). Relative divergence of mobbing calls and songs structures in passerine birds and the importance of acoustic features for localization efficiency. *Journal of Evolutionary Biology*, *soumission prévue octobre 2018*

[6] **Dutour, M.**, & Lengagne, T. Léna, J. P. (2018). Effect of compositional syntax manipulation on heterospecific response to mobbing call. *Behavioral Ecology and Sociobiology*, *soumis août 2018*

Chapitre 3 : Rôle de l'apprentissage dans la mise en place de la réponse aux signaux de harcèlement

[7] **Dutour, M.,** Léna, J.P., Dumet, A., Gardette, V., Mondy, N., & Lengagne, T. (2018). Mobbing in great tit (*Parus major*): the implication of associative learning process, *Animal Behaviour*, *resoumis septembre 2018*

Chapitre 1

Harcèlement des prédateurs : Comment Expliquer la Mise en Place d'une Telle Stratégie par les Proies ?

Article 1 : Mobbing behaviour varies according to predator dangerousness and occurrence

Dutour, M., Léna, J.P., & Lengagne, T.
Animal Behaviour, 119 (2016), 119-124.

Problématique :

Le comportement de harcèlement du prédateur est un comportement surprenant puisqu'il consiste non pas à fuir comme le font la plupart des proies mais à aller vers le prédateur. La dangerosité du prédateur et son occurrence influencent-elles la mise en place de cette réponse comportementale ?

Objectifs :

Dans un premier temps, nous avons évalué comment les oiseaux réagissent face à deux espèces de chouettes assez proches : la chevêchette d'Europe (*Glaucidium passerinum*), grande prédatrice de passereaux et la chouette de tengmalm (*Aegolius funereus*), qui se nourrit principalement de rongeurs. Dans un deuxième temps, nous avons étudié l'expression du comportement de harcèlement au sein des communautés de passereaux lorsque la chevêchette est absente du milieu. Finalement, la réponse à une bande son (= repasse) de cris de harcèlement provenant de quatre espèces de passereaux communs a été étudiée afin de vérifier chez les oiseaux testés que l'absence de réponse à la chevêchette n'est pas due à une disparition du comportement de harcèlement.

Résultats :

- les oiseaux répondent plus à la repasse de la chouette prédatrice (i.e. chevêchette) qu'à la repasse de la chouette représentant un plus faible risque (i.e. tengmalm).
- les oiseaux ne répondent pas à la repasse de la chevêchette sur les sites où elle est absente.
- les oiseaux répondent aux cris de harcèlement sur les sites avec ou sans chevêchette.

Conclusion :

Le comportement de harcèlement envers un prédateur est un trait flexible et dépend de l'expérience. Les résultats suggèrent que la réponse à la repasse de cris de harcèlement varie fortement entre les espèces de passereaux.

Animal Behaviour 119 (2016) 119–124

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Mobbing behaviour varies according to predator dangerousness and occurrence

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Animals possess various antipredator behaviours to reduce their risk of predation. Whereas most prey make considerable effort to avoid their predators, sometimes individuals approach and mob predators as a group. Among the types of predators that elicit mobbing, raptors such as hawks and owls are one of the more consistent targets. We conducted playback experiments to investigate the strength of mobbing behaviour according to the perceived risk associated with either predator dangerousness or local predation pressure. We first determined whether mobbing is specific to dangerous predators or more broadly directed at predatory species. We experimentally investigated whether prey can discriminate the level of dangerousness of two owl species. Our results indicate that prey adjusted the strength of their mobbing behaviour according to the perceived risk: passerine birds mobbed the Eurasian pygmy owl, *Glaucidium passerinum* (i.e. a dangerous predator) but not the boreal owl, *Aegolius funereus* (i.e. a far less dangerous species). Second, we compared mobbing behaviour in similar habitats differing in predation pressure (with or without pygmy owls). Working on identical bird communities, we revealed that mobbing varied in relation to the local presence of the predator. Where the pygmy owl was absent, calls of this dangerous predator failed to elicit mobbing among passerine birds although they responded strongly to a playback of a mobbing chorus. This study provides experimental evidence that intense predation increases the expression of cooperative mobbing in passerine birds.

Typically, once a predator has been detected, prey move away while emitting alarm signals. When hearing alarm calls, animals either flee to hide or remain motionless. More surprisingly, in some situations, prey do not flee but mob predators. Mobbing is defined as movements of prey towards the predator involving both attacks with stereotyped behaviours and easily localizable calls that quickly draw a crowd of both conspecific and heterospecific prey against the predator (Curio, 1978; Hartley, 1950; Hurd, 1996; Randler & Vollmer, 2013). The principal benefit of mobbing is to cooperatively chase the predator away ('move-on hypothesis', Curio, 1978; Pettifor, 1990; Flasskamp, 1994; Pavey & Smyth, 1998) although such strategy is not without risk (Curio & Regelmann, 1986; Dugatkin & Godin, 1992; Sordahl, 1990).

Even though mobbing is not uncommon among vertebrates, how predation risk drives the expression of this behaviour is still poorly understood. Most studies have suggested that animals adjust the strength of their mobbing behaviour according to the perceived risk associated with either predator dangerousness or local predation pressure (Graw & Manser, 2007; Kaplan, Johnson, Koboroff, & Rogers, 2009; Kobayashi, 1987; Koboroff, 2004; Koboroff, Kaplan, & Rogers, 2013). Predator dangerousness, i.e. the rate at which predators kill prey, can greatly vary between predator species, while predatory pressure mostly depends on the abundance of a local predator species. Although mobbing is thought to correlate positively with predator dangerousness, studies on mobbing have only compared prey responses to predators and nonpredatory species (Kobayashi, 1987; Koboroff, 2004; Lind, Jöngren, Nilsson, Schönberg Alm, & Strandmark, 2005). For example, Lind et al. (2005) has experimentally shown that great tits, *Parus major*, do not mob the European robin, *Erithacus rubecula*, i.e. a nonpredatory species, but approach and mob Eurasian pygmy owls, *Glaucidium passerinum*, a predator that is particularly dangerous for great tits. However, inoffensive species such as the European robin can be easily discriminated acoustically from predatory species. Hence, it is still unclear whether mobbing is specific to dangerous predators or more broadly directed at predatory species whatever their dangerousness. It is thus important to investigate the accuracy of prey discrimination facing predatory species of different dangerousness levels (see for instance Griesser, 2009 working at an intraspecific level on the Siberian jay, *Perisoreus infaustus*). Many studies have emphasized that local predation pressure is an excellent predictor of the strength of mobbing

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responses, with birds exhibiting stronger mobbing responses in locations where predators are common and weaker responses where predators are rare (Sandoval & Wilson, 2012; Tilgar & Moks, 2015). This is in agreement with the study of Reudink, Nocera, and Curry (2007) suggesting that birds mob only predatory species they have previously experienced. Interestingly, studies also indicate that prey respond to mobbing calls even in areas where their natural predator is absent (Johnson, McNaughton, Shelley, & Blumstein, 2004; Randler, 2012) suggesting that the convergent features themselves would facilitate interspecific communication (Marler, 1955, 1957). Nevertheless, it is worth noting that comparing behavioural responses between different localities should be interpreted with caution. For instance, prey communities may vary greatly between localities which can make comparisons irrelevant. This can be particularly problematic if the prey species richness or the relative abundance of the most commonly preyed on species vary according to predator occurrence. Unfortunately, to our knowledge, previous studies did not control for such variations in prey communities between the compared sites.

In this study, we conducted a series of playback experiments to determine whether passerine mobbing behaviour depends on local predation risk. First, we studied birds' responses to two morphologically similar owl species to evaluate whether mobbing is specific to predator dangerousness. We used passerine responses to the Eurasian pygmy owl (hereafter pygmy owl), a predator specialized in passerine birds which constitutes an ideal model species for studying mobbing behaviour (Kellomäki, 1977; Kullberg, 1995; Muller & Riols, 2013; Solheim, 1984; Sotnar, Pacenovsky, & Obuch, 2015). We also used the boreal owl, *Aegolius funereus*, a less dangerous species as indicated by the low prevalence of birds in its diet (Korpimäki, 1986). We predicted that passerines should respond more strongly to the pygmy owl than to the boreal owl. Second, we tested mobbing in two forest patches, one with and one without pygmy owls, in the same mountain range and with identical bird communities, to compare mobbing behaviour with different predation pressures. We predicted that birds would not mob in response to predator vocalizations where the predator was absent, because owl calls are not associated with predation. However, it was important to control for the possibility that the absence of response was due to a loss of mobbing ability; hence, in both forest patches (with or without pygmy owls), we tested whether birds responded to the playback of a mobbing chorus.

METHODS

Site and Species Studied

The study was conducted in mixed deciduous-coniferous forests in the Jura mountains (Ain, France) in two study areas. The first is located near Oyonnax (46°15′N, 5°39′E, mean altitude 850 m) where the Eurasian pygmy owl, a dangerous predator of passerine birds, and the boreal owl, a less dangerous predator of passerine birds, are both common. The second study area, in which owls are absent, is located 40 km away from the first (45°57′N, 5°20′E, mean altitude 260 m). Four listening sessions were performed at each site to control for owl occurrence using site occupancy models (Appendix 1). While owls were detected in each site of the first area ($N = 20$), none was detected in the second area ($N = 15$), confirming previous information (Lengagne & Bulliffon, 2014) and making the two sampled areas (hereafter referred as area with owls versus area without owls) highly relevant to investigate the influence of owl predation exposure on mobbing. The distance between the different sites was at least 500 m to avoid a responding individual contributing more than once to the analyses. At each of the 35 sites, bird species diversity was surveyed through a 20 min acoustic census of about 100 m radius around the observer. A census was performed before any experiment (Blondel, Ferry, & Frochot, 1970). In total, 32 passerine species were identified in the area where pygmy owls were present and 22 where pygmy owls were absent. In all cases, we focused on the eight bird species that were most commonly preyed on by pygmy owls (Muller & Riols, 2013): common chaffinch, *Fringilla coelebs*, coal tit, *Periparus ater*, European crested tit, *Lophophanes cristatus*, great tit, blue tit, *Cyanistes caeruleus*, goldcrest, *Regulus regulus*, common firecrest, *Regulus ignicapilla*, and European robin. This passerine community did not vary significantly between the two study areas (see Appendix 2, Fig. A1).

Experimental Design

Data were collected during playback experiments conducted between May and July 2014 (experiment 1) and between September and November 2014 (experiment 2).

Response specificity (experiment 1) was tested in different sites of the area with owls ($N = 20$). For this purpose, we applied a crossover design: at each site, the bird community was offered a broadcast sequence of the following three experimental stimuli, pygmy owl calls, mobbing chorus and boreal owl calls. This study design is particularly convenient for minimizing the error variance resulting from the subject effect (i.e. the bird community present at the site), since the relative effect of stimuli can be assessed within each bird community (Jones & Kenward, 2003). A latency period of 5 min was systematically observed between each experimental test (see test procedure for the complete description) in order to avoid carryover effects (i.e. residual effects of the experimental stimuli tested during the previous period on the next one). The sequence order of the three playback stimuli was also alternated between sites to avoid any bias that could result from the sequence order.

The goal of experiment 2 was to test whether mobbing behaviour of passerine birds varied in relation to predator presence. For this purpose, we selected 15 sites in the area without owls and 15 of the 20 sites in the area with owls that were previously used in experiment 1. Experimental tests were performed as in the first experiment except that the broadcast sequence included only two experimental stimuli: the pygmy owl calls and the mobbing chorus.

Test Procedure

Two observers with binoculars were positioned opposite each other at vantage points at least 10 m from the playback (i.e. focal zone) and collected data for 13 min (duration of a test). During the first 5 min we identified and counted all the birds present in the focal zone close to the loudspeaker; these observed birds were excluded from counts in subsequent analyses. Such observations were rare (2.2% of total observed birds). Then, during the 3 min playback, we quantified the birds' response using the number of species observed within a 10 m radius of the loudspeaker. After the playback, observers waited for 5 min before beginning the next test.

Experimental Stimuli

We broadcast playbacks via an amplified loudspeaker (SMC8060, Beyma) connected to a digital playback device (WAV player). Playbacks were restricted to 0600–1200 hours, which corresponds to a period of high activity in birds. To avoid pseudoreplication, we first tested whether prey response was specific to a particular soundtrack or generalizable to various soundtracks of the same species. For both owl species, we downloaded from online databases of avian sounds (http://www.xeno-canto.org) two soundtracks recorded in two populations located on both sides of the species' range in order to encompass the call variation range that a local prey community could experience. Both the call variability within each soundtrack and the call variation between pairs of soundtracks were controlled a posteriori (results not shown). Results showed that passerine responses (i.e. number of species observed) to pygmy owl calls recorded in Switzerland or Sweden were the same whatever the soundtrack used (permutation test: $t = -1.48$, $N = 12$, $P = 0.20$). In addition, the proportion of species that responded to boreal owl calls recorded in Denmark or France was close to zero ($N = 12$ sites). Hence our results were not due to a particular soundtrack (no pseudoreplication). Although it was easy to ensure that pygmy owl or boreal owl soundtracks had the same 'predator value' for passerines, the mobbing chorus recorded in the field may have differed in ways (intensity, species composition) difficult for a human observer to measure. To avoid this problem, we built a soundtrack corresponding to a mixture of four different bird species. Building an artificial manipulated stimulus ensured that we avoided any pseudoreplication problem and that passerine birds would all be tested with the same threat. We used multispecies bouts of mobbing chorus (common chaffinch, coal tit, European crested tit and great tit) recorded in response to a pygmy owl song with a Fostex FR2LE digital recorder connected to a Sennheiser ME62-K6 microphone.

Statistical Analysis

All analyses were done using the SAS 9.3 software (SAS Institute Inc., Cary, NC, U.S.A.). To investigate the relative effect of predator dangerousness and mobbing chorus (experiment 1), we tested whether the proportion of mobbing species varied within each site according to the experimental stimuli sequentially presented (i.e. pygmy owl call, boreal owl call and mobbing chorus). These analyses were performed using a log linear mixed model (LLMM, Procedure GLIMMIX, SAS Institute Inc.). More specifically, we modelled the proportion of mobbing species using the number of responding species as the dependent variable with a Poisson distribution for the error term specification and the number of bird species inventoried at the experimental location (i.e. site) as the offset covariate. The experimental stimulus was introduced as an explanatory factor in the fixed part of the model. Since our experiment was designed to assess the relative effect of the three stimuli within the bird community located at each site, we treated the site as a random effect. To check for a possible carryover effect, the presentation order of the experimental stimuli (i.e. three modalities: first, second or third) and the sequence order of the three stimuli (i.e. six combination orders) were also included as factors in the fixed part of the model. The significance of each explanatory term was tested using a nonsequential F test and the Kenward–Roger method was used to estimate the degrees of freedom. Nonsignificant terms were then removed to obtain the final model. Proportions of mobbing species were then compared between the experimental stimuli using the contrast method. We used a similar approach to investigate whether the local occurrence of the predator had any effect on the proportion of species responding either to the predator stimuli or to a mobbing chorus. As above, sites were introduced in the model as a random effect. The experimental stimulus (i.e. pygmy owl call versus mobbing chorus), the study area (with versus without predator) and their interactive effect were introduced as explanatory terms in the fixed part of the model.

Ethical Note

Although our playbacks experiments changed the behaviour of the targeted birds, we do not feel that these experiments were stressful. Indeed, birds recovered normal activity and were not present near the loudspeaker 5 min after our experiments. All behavioural observations performed during this study complied with the legal requirements in France and followed the ASAB/ABS Guidelines for the Use of Animals in Research. The study was approved by the DREAL supervisor and permit no. 69266347 of the Direction des Services Vétérinaires.

RESULTS

Mobbing Response and Predator Dangerousness (experiment 1)

There was no significant carryover effect in bird responses (LLMM: treatment position: $F_{2,35.5} = 0.16$, $P = 0.85$; sequence: $F_{5,21.76} = 0.82$, $P = 0.55$). In addition, there was no variation in mobbing according to the presentation order between pygmy owl and mobbing chorus playbacks ($t = 1.94$, $P = 0.12$). The playback type (call of pygmy owl, call of mobbing chorus and call of boreal owl) had a significant effect on bird responses (LLMM: $F_{2,39.83} = 10.51$, $P = 0.0002$; Fig. 1). Indeed, bird species mobbed the pygmy owl more intensely than the boreal owl ($F_{1,45.6} = 20.92$, $P < 0.0001$). Bird species also responded more to mobbing chorus playback than to boreal owl playback ($F_{1,45.29} = 19.61$, $P < 0.0001$), the latter response being close to zero (0.013). In addition, mobbing did not differ between pygmy owl and mobbing chorus playbacks (proportion of species = 0.229 for pygmy owl, 0.249 for mobbing chorus; $F_{1,34.54} = 0.15$, $P = 0.70$). The average number of bird species detected in the test was 2.30 ± 1.30 (corresponding to 5.1 ± 3.67 individuals) during pygmy owl playback and 2.25 ± 0.97 (corresponding to 4.8 ± 2.88 individuals) during mobbing chorus playback.

Mobbing Response and Predation Pressure (experiment 2)

Bird species response was significantly affected by the interaction between the type of stimulus that was broadcast and the presence of the pygmy owl (LLMM: $F_{1,45.88} = 32.48$, $P < 0.0001$; Fig. 2). Species observed in the area where the pygmy owl was present were 12.8 times more likely to respond to a pygmy owl call than species observed in the area where the pygmy owl was absent (contrast test: $F_{1,55.79} = 32.54$, $P < 0.0001$). However, we found that the proportion of species responding to a mobbing chorus did not differ significantly between the two study areas (contrast test: $F_{1,55.79} = 0.37$, $P = 0.21$).

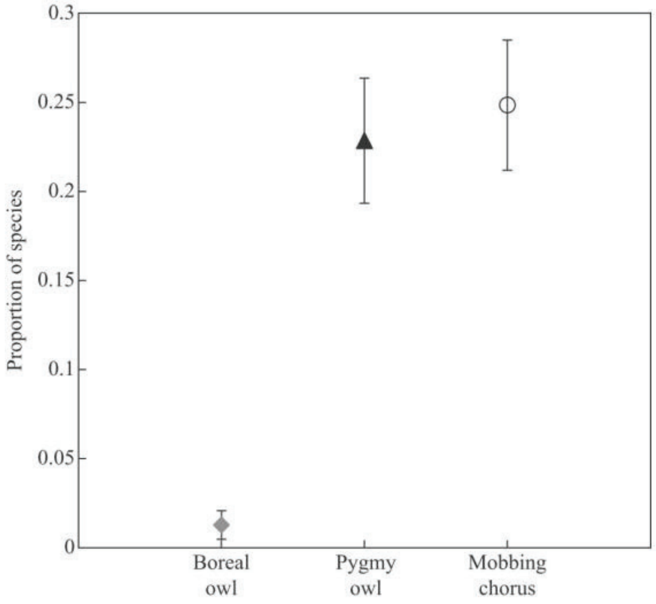

Figure 1. Proportion of species responding to the presentations of a boreal owl (grey diamond), a pygmy owl (black triangle) and mobbing chorus (white circle) calls at sites where owls were present ($N = 20$ sites). Error bars represent SEs.

DISCUSSION

In the present study, we tested the effects of pygmy owl predation on the mobbing behaviour of passerine birds. We showed experimentally that bird responses varied with predation risk (predator dangerousness and presence) and that prey responded to a mobbing chorus even in areas in which these predators were absent.

Several studies have shown that prey respond to predators by adopting behaviours specific to the perceived risk (Graw & Manser, 2007; Kaplan et al., 2009; Kobayashi, 1987; Koboroff, 2004; Koboroff et al., 2013; Lind et al., 2005). However, most of these studies have opposed predator species and inoffensive species such as quails, *Coturnix* sp., tortoises, *Pseudemys scripta*, or parrots, *Platycercus eximius*. In the present study, we have shown that birds responded selectively to the presentation of predator calls according to predator dangerousness: passerine birds mobbed the pygmy owl (i.e. a dangerous predator) but not the boreal owl (i.e. a far less dangerous species). Although we used only two distinct soundtracks per species, it is unlikely that our results are confounded by pseudoreplication because the birds' response did not differ between soundtracks even though these differed substantially. Our results therefore indicate that prey adjusted the strength of their mobbing behaviour according to the perceived risk. The low predatory risk associated with the boreal owl is probably related to its hunting strategy. Indeed, while pygmy owls are diurnal (Cramp, 1985; Mikkola, 1983) and have flexible hunting strategies, boreal owls are nocturnal with a single hunting strategy. Hence, it is not surprising that passerine birds display a differential mobbing response according to owl species. Our results are also congruent with the field study of Morosinotto, Thomson, and Korpimaki (2009) showing that pied flycatchers, *Ficedula hypoleuca*, strongly avoid the territories of pygmy owls but not those of boreal owls for settling. If it is now clear that bird mobbing varies with predator dangerousness, which level of dangerousness is required to elicit mobbing in the prey community remains unclear. In our study, birds did not respond to the boreal owl while the proportion of passerines in the diet of this predator estimated near our study area is about 0.3 (Henrioux, 2014a; versus 0.58 in the pygmy owl diet; Henrioux, 2014b). Although comparisons between studied models should be interpreted with caution, Kaplan et al. (2009) found that birds mob the monitor lizard, *Varanus varius*, while these birds constitute only 0.14–0.16 of the predator's diet. It therefore seems likely that the threshold value of 'dangerousness' above which mobbing is elicited is relatively low. Similarly, one should also expect some variation in mobbing across the prey community, since the relative risk of predation may vary between prey species. For instance, field studies conducted on commonly preyed on bird species have found a relationship between how often a species mobs predators and how often predators prey upon this species (Courter & Ritchison, 2012; Gehlbach, 1994). Investigating more precisely the correlation between the relative prevalence of a species in a predator's diet and its relative involvement in mobbing could thus be particularly insightful.

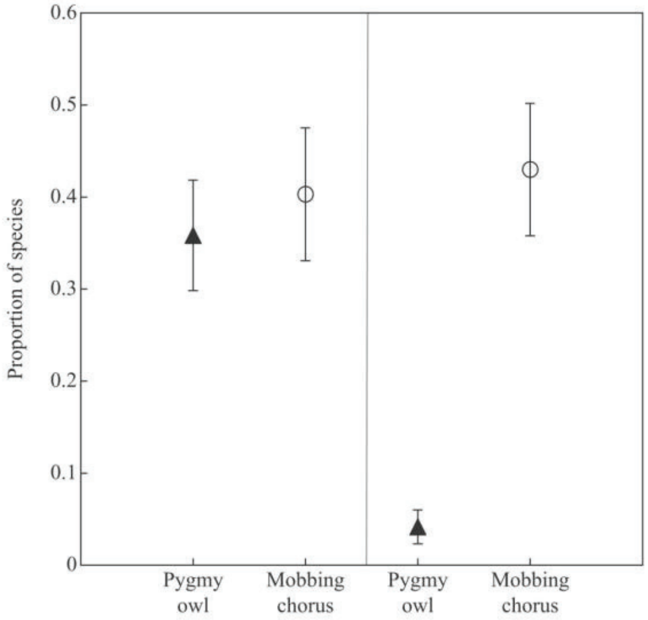

Figure 2. Proportion of species responding to the presentations of a pygmy owl (black triangle) and a mobbing chorus (white circle) calls at sites where the pygmy owl was present (on the left side, $N = 15$ sites) and sites where the pygmy owl was absent (on the right side, $N = 15$ sites). Error bars represent SEs.

Our results also reveal that mobbing varied in relation to the local presence of the predator. In the locations where the pygmy owl was absent, calls of this dangerous predator failed to elicit mobbing among passerine birds. This result is in agreement with Reudink et al. (2007). In their study, tropical birds living in environments devoid of predators often expressed inappropriate antipredator behaviours. Moreover, recent studies have experimentally shown that local predation pressure can predict the strength of mobbing responses in birds: individuals exhibit a stronger mobbing response when local predation pressure is high (Krams et al., 2010; Sandoval & Wilson, 2012; Tilgar & Moks, 2015). However, these authors did not take into account the number of species present before tests began. We did this in our study, so were able to control for available prey and predators. The predatory response where the pygmy owl is a common predator is linked either to a selection process (local adaptation) or to a learning process. In the first case, only one recent study, in Alpine swifts, *Apus melba*, has shown that antipredator behaviour is heritable (Bize, Diaz, & Lindström, 2012). In many situations, it is most probable that offspring may learn to adjust their behaviour and to express a mobbing response by observing their conspecifics' mobbing behaviour (Curio, 1978; Francis, Hailman, & Woolfenden, 1989; Graw & Manser, 2007). For example, in an experimental study, Campbell and Snowdon (2009) showed that captive-reared cottontop tamarins, *Saguinus oedipus*, do not innately recognize predators and a demonstrator seems to be necessary to acquire predator recognition. Hence, the fine-tuning of this behaviour probably depends on experience. In our case, we cannot determine whether bird mobbing behaviour observed in areas with pygmy owls results from an innate or a learned process. Experiments involving passerine eggs transferred from areas where pygmy owls are present to areas without owls would answer this question.

As predicted, prey responded to a mobbing chorus whether or not pygmy owls were present in the area, a result that is in agreement with previous studies on other predators known to elicit mobbing (Johnson et al., 2004; Randler, 2012). The most likely explanation for the similar response to a mobbing chorus regardless of whether the studied predator species is present is that numerous predator species are known to elicit mobbing behaviour (Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Curio, Klump, & Regelmann, 1983). Thus, in a multipredator environment, mobbing behaviours could be maintained even in the absence of a specific predator species. This is probably particularly true for avian prey given the ubiquity of opportunist nest predators. These predators can be expected to favour mobbing since they do not usually represent an immediate danger for the adults but are particularly dangerous for offspring. More surprisingly, our results have also shown that the strength of passerine response to a mobbing chorus was not significantly higher than that to the pygmy owl calls in the area where this predator was present. Indeed, a previous study has reported that the mobbing calls elicited a stronger response than that elicited by a specific dangerous predator, suggesting that mobbing calls give information not only on the presence of the predator, but also on the response of other prey species perceiving the situation as threatening (Sandoval & Wilson, 2012). Previous studies have also suggested that mobbing calls contain information about the degree of threat that a predator represents (Billings, Greene, & LuciaJensen, 2015; Graw & Manser, 2007; Griesser, 2009; Koboroff et al., 2013; Naguib et al., 1999; Suzuki, 2014; Templeton, Greene, & Davis, 2005). The difference in the method used to infer the strength of the response may well explain why our results differ from those reported in previous studies (Sandoval & Wilson, 2012). In particular, our measure of mobbing response is probably more conservative than that used by Sandoval and Wilson (2012), since we did not use the number of individuals attracted by the mobbing call but the proportion of responding species among species present at the experimental location.

Mixed-species avian mobbing is a widely recognized phenomenon. Mobbing calls can communicate the presence of a predator to heterospecifics as well as conspecifics (Forsman & Mönkkönen, 2001; Hetrick & Sieving, 2012; Hurd, 1996; Marler, 1957; Randler & Vollmer, 2013; Randler & Förschler, 2011; Sandoval & Wilson, 2012; Templeton & Greene, 2007; Zimmermann & Curio, 1988). Indeed, our soundtrack of the mobbing chorus with four species elicited a response not only from these four species but also from all the other species strongly predated by the pygmy owl. In our study, the proportion of conspecific species (i.e. four species of the mobbing chorus playback) that responded to the mobbing choruses was 0.697 whereas the proportion of heterospecific species (i.e. four species not included in the mobbing chorus playback) was 0.375. However, responses to mobbing choruses vary greatly between heterospecific passerine species. For example, in our experiments, the goldcrest responded in 20 of 24 tests where it was present whereas the European robin responded in only two of 32 tests where it was present. Hence, we emphasize heterospecific communication and our results suggest that responses are asymmetrical across species. In future experiments we will investigate the underlying processes of the response to mobbing calls.

In conclusion, we have shown that passerines responded to a mobbing chorus regardless of the presence of dangerous predators in the area, suggesting that it is a conserved trait. In this case, the removal of one predator should have limited effect on the persistence of the antipredator strategy because predation pressure is usually not due to a single species. On the other hand, the absence of passerine response to owls in the area where these predators were absent suggests that mobbing behaviour against owls is an experience-dependent and highly flexible trait. Future studies should explore the costs and benefits of mobbing at species level to assess to what extent this trait is flexible.

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APPENDIX 1. SITE OCCUPANCY MODEL (EURASIAN PYGMY OWL)

Model selection was based on Akaike's information criterion (AIC). The model including study area as covariate was considered best ($\Delta AIC = 29.26$) and showed that the occurrence of pygmy owls was 1 in areas where the pygmy owl was present and 0 in areas where the pygmy owl was absent.

APPENDIX 2. SPECIES RICHNESS IN AREAS WITH OR WITHOUT OWL

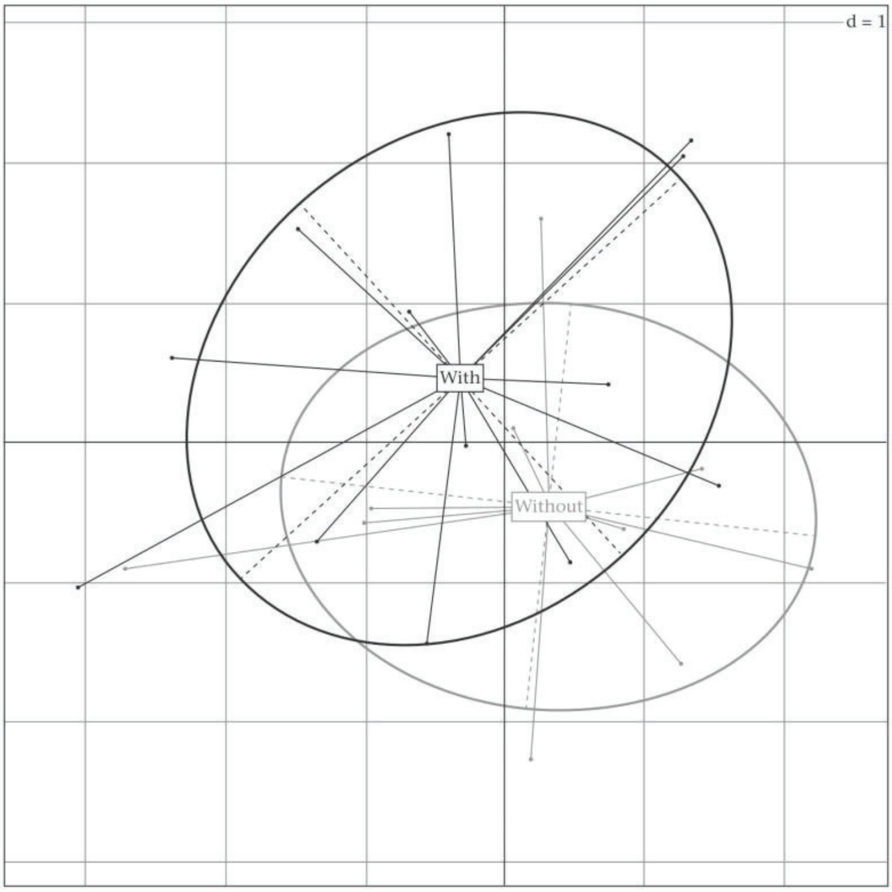

Figure A1. Schematic representation of factor correspondence analysis (FCA) of the bird species most frequently killed by Eurasian pygmy owls in areas with (black) and without (grey) owls (FCA1: 25.27%; FCA2: 21.45%).

Article 2 : Mobbing behaviour in a passerine community increases with prevalence in predator diet

Dutour, M., Léna, J.P., & Lengagne, T.
Ibis, 159 (2017), 324-330.

Problématique :

Chez les passereaux, le harcèlement consiste à approcher le prédateur, l'encercler et parfois même l'attaquer directement. Les animaux ajustent la force de leur comportement de harcèlement en fonction du risque de prédation perçu. Le fait d'être régulièrement consommé par un prédateur augmente-t-il l'intensité du comportement de harcèlement ?

Objectifs :

L'objectif est d'étudier les effets de la prédation de la chevêchette sur l'expression du comportement de harcèlement de 22 espèces de passereaux. Nous avons étudié la réponse des oiseaux en prenant en compte deux paramètres : l'appartenance au régime alimentaire du prédateur et la saison (printemps et automne).

Résultats :

- la réponse des 22 espèces est liée au régime alimentaire de la chevêchette : les espèces qui répondent le plus au prédateur sont celles qui subissent la plus forte prédation.
- l'intensité du harcèlement est plus importante pendant l'automne que pendant le printemps.

Conclusion :

Notre étude montre que la mise en place de cette réponse est liée au risque de se faire manger et souligne l'importance de considérer la saison pour l'étude du comportement de harcèlement.

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Mobbing behaviour in a passerine community increases with prevalence in predator diet

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Mobbing behaviour against predators is well documented but less is known about the factors influencing variation in behavioural response between prey species. We conducted a series of playback experiments to examine how the mobbing responses of prey species differed according to their relative risk of predation by the Eurasian Pygmy Owl *Glaucidium passerinum*, a predator of passerines. We found that mobbing among 22 passerine prey species was positively correlated with their prevalence in the Pygmy Owl diet. To compare mobbing behaviour between two seasons, we conducted playback experiments during spring (breeding season) and autumn (non-breeding season). Contrary to previous studies, we found that mobbing intensity was greater during autumn than in spring. Our study shows a differential mobbing response of 22 species to the calls from one predator species and underscores the importance of considering seasonal variation in mobbing behaviour. Mobbing response differences observed among bird species strongly suggest different cooperation behaviour at the community level.

Keywords: Eurasian Pygmy Owl, *Glaucidium passerinum*, mobbing behaviour, passerine, playback experiments.

When a predator is nearby or attacks, many bird species give alarm calls (Klump & Shalter 1984, Zuberbühler 2009). These calls are often classified as ‘flee’ alarm calls, which are associated with immediate escape, or ‘mobbing’ alarm calls, which are associated with individuals approaching to repel a potential predator (Hartley 1950, Curio 1978, Hurd 1996). Mobbing calls are broadband in structure, making them easy to localize (Marler 1955, Klump & Shalter 1984, Ficken & Popp 1996, Jones & Hill 2001), and are effective in attracting conspecific and heterospecific individuals to join a communal response to the predator (Hartley 1950, Curio 1978, Hurd 1996, Krams *et al.* 2006). Mobbing can be beneficial and may cause a predator to leave an area (the ‘move-on hypothesis’; Curio 1978, Pettifor 1990, Flasskamp 1994, Pavey & Smyth 1998), but may also be costly by increasing the risk of injury or death to the mobbing individual (Curio & Regelmann 1986, Sordahl 1990, Dugatkin & Godin 1992). Animals adjust the strength of their mobbing behaviour according to the perceived risk associated with the predator’s threat level (Koboroff *et al.* 2013, Billings *et al.* 2015, Dutour *et al.* 2016).

Mobbing is a widespread defensive tactic in birds, and heterospecific mobbing of raptors is common in passerine communities (Altmann 1956, Curio *et al.* 1978, 1983, Gehlbach & Leverett 1995). Raptors preying on birds are more heavily mobbed than other birds of prey (Dutour *et al.* 2016) but mobbing response can vary substantially among prey species according to their respective risk of predation (Shedd 1983). For example, Courter and Ritchison (2012) found that raptors preying more on Tufted Titmice *Baeolophus bicolor* than on Carolina Chickadees *Poecile carolinensis* elicit heavier mobbing from the Titmouse than from the Chickadee. Mobbing activity also varies seasonally and is often most intense during the breeding season to deter nest predators and to teach offspring predator-specific defence

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strategies (Curio *et al.* 1978, Vieth *et al.* 1980, Frankenberg 1981, Zimmermann & Curio 1988, Gehlbach & Leverett 1995). However, comparisons of behavioural responses between seasons should be interpreted cautiously because prey communities and the risk of predation of component species may vary between seasons; previous studies have not controlled for variations in prey communities when comparing mobbing behaviour between seasons.

Owls in the genus *Glaucidium* prey mainly on passerine birds, making them particularly suited to study the mobbing behaviour in passerine communities. For example, in tropical forests of southern Brazil, the Ferruginous Pygmy Owl *Glaucidium brasilianum* is often mobbed by a wide range of avian species (Shalter 1978, Motta-Junior 2007, Sandoval & Wilson 2012, Cunha *et al.* 2013, Tilgar & Moks 2015), as is the Northern Pygmy Owl *Glaucidium californicum* in North America (Deppe *et al.* 2003, Templeton *et al.* 2005, Templeton & Greene 2007, Nocera & Ratcliffe 2010, Billings *et al.* 2015). In Europe, the Eurasian Pygmy Owl *Glaucidium passerinum* (hereafter Pygmy Owl) also specializes in feeding on birds (Solheim 1984, Kullberg 1995, Sotnar *et al.* 2015), including fledglings (Likachev 1971, Kellomäki 1977, Sotnar *et al.* 2015), some of which may be pulled from nest-holes (Möckel & Möckel 1984).

We conducted a series of playback experiments to examine to what extent the mobbing response exhibited by prey species varies according to their respective risk of predation by Pygmy Owls. We predicted that the expression of mobbing behaviour in a species would be positively correlated with its prevalence in Pygmy Owl diet and that mobbing against Pygmy Owls should be more important during the songbird breeding season in the spring than during autumn.

MATERIALS AND METHODS

Study site

We studied a community of wild passerines in mixed forests near Oyonnax (Ain, France, 46°15′N, 5°39′E). The Pygmy Owl is common in the study area (Dutour *et al.* 2016). In total, 20 sites occupied by the species were chosen for the experiment. Observations of calling individuals in spring at these sites suggested that they were occupied by breeding owls. Additionally, four listening sessions were undertaken during autumn at each site to confirm the presence of Pygmy Owls. The distance between sites was at least 500 m to minimize the risk that the same individual passerines would be present at different sites.

Experimental design

Playback experiments were conducted between May and July 2014 (spring) and between September and November 2014 (autumn). At each of the sites, and before each playback session, bird species diversity was surveyed through a 20-min census of 100 m radius around the observer using both acoustic and visual cues (Blondel *et al.* 1970). In total, 28 and 26 passerine species were identified respectively during spring and autumn. All data analysis focuses on the 22 resident bird species, which were classified according to their prevalence in Pygmy Owl diet (never eaten, occasionally eaten, very often eaten; Muller & Riols 2013; Table 1).

To assess whether mobbing behaviour of passerine birds varied in relation to Pygmy Owl diet and season, we broadcast a series of Pygmy Owl calls at 20 sites in spring and at 15 sites in autumn. Two observers with binoculars were positioned opposite each other at vantage points at least 10 m from the playback (i.e. focal zone) and collected data for 8 min (duration of a test). During the first 5 min (pre-experiment) we identified and counted all the birds already present in the focal zone. Because mobbing activity could not be inferred for these individuals already close to the loudspeaker before playback began, these observations were discarded from subsequent analyses (1.35% of total observed birds). Then, during the 3 min of playback, we quantified avian response using the number of species observed within a 10-m radius of the loudspeaker. We studied mobbing behaviour at a community scale and performed our tests on a population of wild passerines in mixed deciduous–coniferous forests. For these reasons, we only looked at flying movements and not the second characteristic of mobbing, calling behaviour. Indeed, as noted by Sandoval and Wilson (2012) it was not possible to ensure which bird is calling or not (sometimes more than 10 birds were flying around the loudspeaker). Mobbing response was a binary response: 'Yes' if an individual of a previously detected species approached within 10 m of the speaker during

Table 1. Details of 22 species identified during 20-min censuses before playback experiments.

Species	Common name	Diet	Spring	Autumn
Garrulus glandarius	Eurasian Jay	N	3	2
Coccothraustes coccothraustes	Hawfinch	N	0	1
Nucifraga caryocatactes	Spotted Nutcracker	N	2	2
Turdus merula	Common Blackbird	N	7	4
Pyrrhula pyrrhula	Eurasian Bullfinch	O	9	8
Sitta europaea	Eurasian Nuthatch	O	3	1
Troglodytes troglodytes	Eurasian Wren	O	10	5
Certhia familiaris	Eurasian Treecreeper	O	2	1
Certhia brachydactyla	Short-toed Treecreeper	O	0	2
Aegithalos caudatus	Long-tail Tit	O	0	2
Turdus viscivorus	Mistle Thrush	O	0	4
Loxia curvirostra	Red Crossbill	O	2	11
Turdus philomelos	Song Thrush	O	7	0
Poecile montanus	Willow Tit	O	2	5
Cyanistes caeruleus	Blue Tit	V	1	10
Periparus ater	Coal Tit	V	15	12
Fringilla coelebs	Common Chaffinch	V	15	11
Regulus ignicapilla	Common Firecrest	V	6	2
Lophophanes cristatus	European Crested Tit	V	9	13
Erithacus rubecula	European Robin	V	11	7
Regulus regulus	Goldcrest	V	5	8
Parus major	Great Tit	V	3	14

Birds were classified according to their prevalence in Eurasian Pygmy Owl diet (three groups: N – never eaten, O – occasionally eaten, V – very often eaten). This table includes the detection of species in each season, corresponding to how many of the 22 species were detected on the same studied sites in spring and during autumn (n = 15 sites).

the playback; 'No' if no individual of a previously detected species approached within 10 m of the speaker during the playback.

Experimental stimuli

We broadcast playbacks at 80 dB(C) via an amplified loudspeaker (SMC8060 Beyma and Audiophonic TA2024 amplifier) connected to a digital playback device (WAV player). In the field, amplitude level was matched by ear to correspond to natural calls made by Pygmy Owls and the same output level was used on our electronic device for all tests. At the end of the experiment we measured the value used during tests by way of a sound level meter (LT Lutron SL-4001, C weighting, slow settings, re: 20μPa). Playbacks were performed during calm and dry weather to improve calling probability in birds (Lengagne & Slater 2002) and restricted to 06:00–12:00 h, which corresponds to a period of high activity in birds. The owl calls were obtained from online databases of avian sounds (http://www.xeno-canto.org) for which we have already shown that passerine response was the same regardless of the soundtrack used (Dutour *et al.* 2016). The soundtrack of 3 min corresponded to a call sequence of 75 Pygmy Owl calls.

Data analysis

All analyses were carried out using SAS 9.3 software. None of the species classified as 'never eaten' (n = 4 in spring and in autumn) responded to Pygmy Owl calls in either season. We therefore compared the proportion of responding species between the 'never eaten' group and the other two groups ('occasionally' and 'often' eaten) using non-parametric, permutation-based, Wilcoxon tests. We then compared species responses between the 'occasionally' (n = 10) and the 'often' eaten (n = 8) groups. We focused on birds detected in the vicinity of the test location (i.e. detected during the preceding census) to calculate a response probability for each present species. Indeed, if a species has not been detected in the immediate vicinity of the playback place, it was not possible to determine whether this species did not respond to our playback or was absent. For each species, we therefore recorded whether a species was mobbing or not at each site, given that it was present at the site during the test. Of a total of 275 mobbing responses recorded in the 18 species during spring and autumn, 25 came from species not detected in the survey immediately preceding the playback test. Whether these 25 observations were included in the analyses did not change significantly the results, and we therefore discarded these observations from analyses to avoid over-representation of these species compared with undetected ones that did not respond. We used a logistic linear mixed model treating the species response observed at each site (mobbing response = 1; no mobbing response = 0) as a repeated measurement of the species propensity to mob. Species ($n = 18$) were introduced in the model as a random effect. Because the species composition (i.e. the species that were present during the test) varies between locations and also between seasons for a same location, we did not introduce a site random effect in the model. The season (spring vs. autumn), the prevalence in the diet ('occasionally' eaten vs. 'often' eaten) and the interaction between season and diet prevalence were introduced as explanatory terms in the fixed part of the model. The significance of each explanatory term was tested using a non-sequential *F*-test and the Kenward–Rogers method was used to approximate the denominator degree of freedom. Non-significant terms ($P > 0.05$) were removed to reach the final model and contrast analyses were performed to investigate the magnitude of each effect.

RESULTS

Species prevalence in the Eurasian Pygmy Owl diet and seasonal variations

Non-parametric tests showed that the proportion of species responding to the owl call was significantly lower in the 'never eaten' group than in the other two groups combined in both seasons (permutation test for spring; $n = 15$, $P = 0.0019$ and autumn; $n = 10$, $P = 0.0014$; Fig. 1). Focusing on the prey species recorded in the diet of the Pygmy Owl, our analyses showed that both the prevalence of the bird species in the diet of the owl and season have a significant additive effect on the proportion of bird species which exhibited mobbing behaviour, as assessed by proximity to the loudspeaker during the playback experiment (250 records on 18 species; dietary prevalence effect: $F_{1,17.45} = 7.22$, $P = 0.015$; season effect: $F_{1,247} = 4.09$, $P = 0.044$; interaction term: $F_{1,246} = 0.84$, $P = 0.36$). Contrast analyses indicated that 'often' eaten species mobbed 12.2 times more than 'occasionally' eaten species (95% CI 1.71–83.33) and that species mobbed 2.14 times more during the autumn than they did during the spring (95% CI 1.02–4.49). Finally, as indicated by the substantial random effect of species identity (i.e. 2.21 ± se 1.13), our analyses also suggested a non-negligible variation of the propensity to mob between species within groups and within a same season.

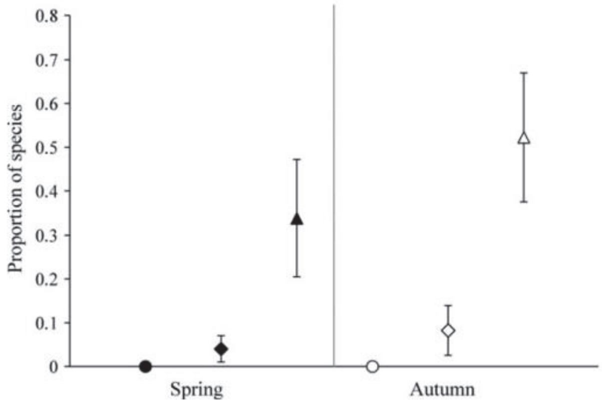

Figure 1. Proportion of bird species responding to Pygmy Owl calls as a function of relationship in the Pygmy Owl diet (never eaten (circle), occasionally eaten (diamond), often eaten (triangle)) of birds for spring (black) and autumn (white) (n = 22 species). Error bars represent standard errors.

DISCUSSION

Our playback experiments showed that mobbing intensity in a species was associated with its prevalence in Pygmy Owl diet; the more a species was preyed upon, the more likely it was to exhibit a mobbing response. Whereas prey species mobbed intensely when they detected Pygmy Owl call playback, species not known to be preyed upon by Pygmy Owls were never seen mobbing the loudspeaker. These results concur with those of Courter and Ritchison (2012) focusing on two prey species, and those of Gehlbach (1994), who recorded the mobbing response among a larger prey species community (17 species) as in the present study. However, in those studies, the relative abundance of the different species at the study site was unknown, making it difficult to distinguish between the mobbing propensity of each species and their respective prevalence and abundance at the study site. Indeed, species observed to be less responsive could simply be the least common in the bird community. In the present study, we controlled for local presence of species at each site of experimental playback so that our results are less likely to be confounded by variation in species occurrence across the study sites.

Among bird species present in the diet of the owl, mobbing response was significantly greater in the autumn than in the spring. This result does not agree with previous studies which have suggested increased mobbing activity during the breeding season (Bolles 1890, Edwards *et al.* 1949, Root 1969, Curio 1975). One possible explanation is that we performed our playback experiments mainly in June. Although several species such as Great Tit *Parus major* and Crested Tit *Lophophanes cristatus* were still breeding, others such as European Robin *Erithacus rubecula* and Mistle Thrush *Turdus viscivorus* had reached the end of the breeding season. Nevertheless, such a bias should have resulted in a similar mobbing activity between seasons rather than an increased mobbing intensity during autumn. Because we used a census method based largely on acoustic cues to detect birds present at the study sites, species occurrence may be underestimated in autumn, when territorial defence is less marked. Hence, if undetected species are less prone to mob than detected species, reduced species detectability in autumn could inflate estimates of mobbing probability in a sample of species at this season. Although our data do not allow us to estimate such a possible bias, we note that among the 25 false absences (i.e. a species found to respond to the playback stimuli despite being undetected at the beginning of the test), eight occurred during the spring session and 17 during the autumn session. These results therefore suggest that our detection probability was indeed lower in autumn than during the spring. Nevertheless, our results were left unchanged when including these 25 false absences (M. Dutour unpubl. data) and it is thus unlikely that undetected species during the autumn session were less prone to mob than were the detected ones. Alternatively, higher mobbing intensity could be due to the higher number of potential bird prey in autumn than in spring. Indeed, during our bird census carried out just before our behavioural tests, we observed a slight increase in the number of 'often' eaten bird species in autumn (Table 1). It remains possible that a higher number of prey species increases the propensity of birds to react and thus increases the strength of the mobbing (Sieving *et al.* 2004).

Ultimately, an increased mobbing activity during autumn could be explained by a seasonal variation of the owl diet, as predation pressure on passerine birds is probably different across seasons. Pygmy Owls are found in mountains or in the northern parts of Europe, where autumn and winter are usually cold and snowy. The deep snow cover protects small mammals against aerial predators, limiting the hunting opportunities available to owls, and driving up the number of passerines killed by Pygmy Owls. In boreal coniferous forests, the Pygmy Owl was found to be the main predator of passerines during winter (Mikkola 1983, Solheim 1984), which was probably also the case in our study area (Y. Muller, pers. comm.). Although it is known that this predator hoards prey such as voles or birds in cavities and nestboxes (Kellomäki 1977, Solheim 1984, Suhonen *et al.* 2007), snow cover and precipitation dramatically lowers the number of hoarded rodents (Terraube *et al.* 2016). This clearly suggests that the bird predation rate was higher during autumn and winter than during the spring. Hence, the change in predation pressure over the course of the year is probably the main explanation of our results, although we know that other factors, including the proximity of the predator (Cresswell 1993, Kleindorfer *et al.* 2005), its posture (Hamerstrom 1957, Coss & Ramakrishnan 2000) and its behaviour (Lind *et al.* 2005, Nolen & Lucas 2009), can also explain the strength of the mobbing. In addition, differences in the response obtained are not the same according to the sensory modality used. For instance, Courter and Ritchison (2012) used skins of the Eastern Screech Owl *Megascops asio* to elicit mobbing behaviour. Using the same biological model, Nolen and Lucas (2009) presented a visual model coupled with playback of monotonic trill and found that several bird species do not react in the same way as previously. Hence, the protocol used can provide a distorted picture of the behaviour of individuals tested (Knight & Temple 1986, Loughry 1987). Thus, it may be difficult to generalize the outcome of an experimental manipulation, especially when no natural encounters are available for comparison. Future studies should now explore the precise cues that elicit a mobbing behaviour at individual level.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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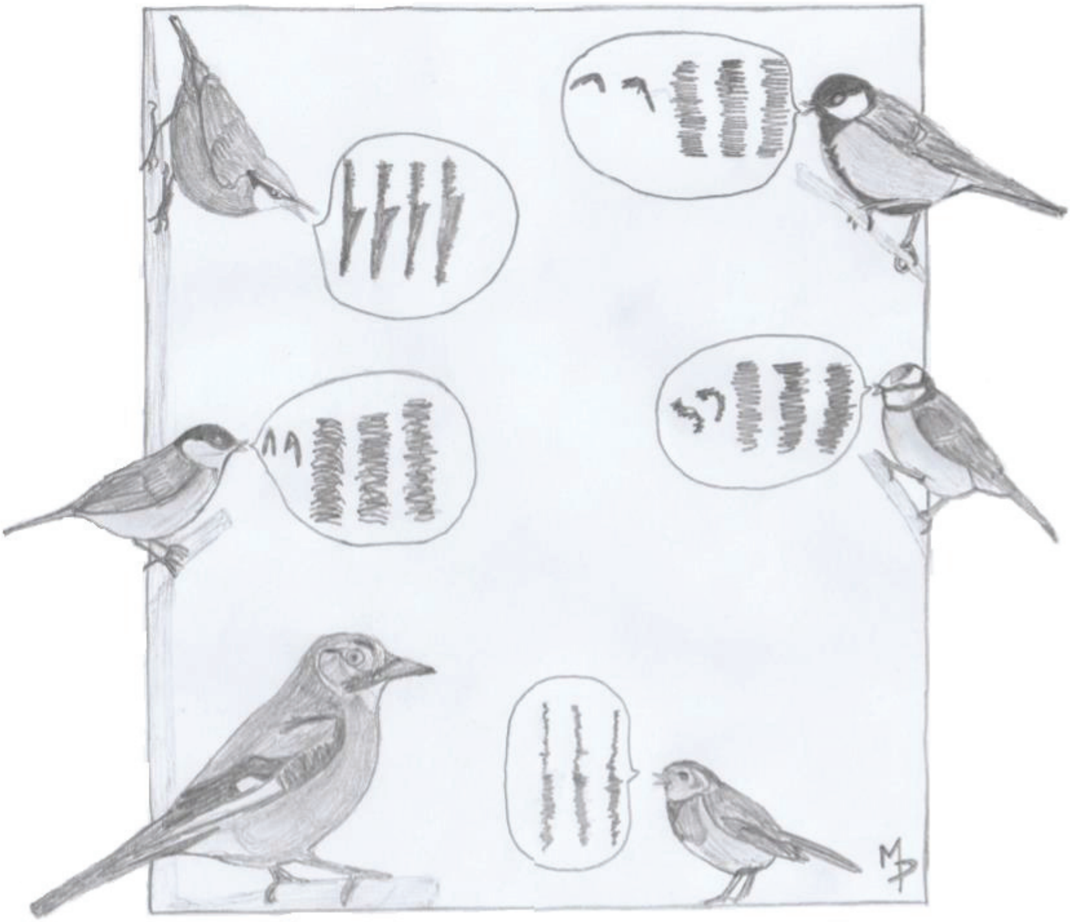
Chapitre 2

Appeler au Harcèlement : une Communication Tournée à la fois vers les Conspécifiques et les Hétérospécifiques



Article 3 : Seasonal variation in mobbing behaviour of passerine birds

Dutour, M., Cordonnier, M., Léna, J.P., & Lengagne, T.
Journal of Ornithology, *resoumission août 2018*.

Problématique :

Lorsqu'ils harcèlent un prédateur, les oiseaux émettent des cris de harcèlement dans le but d'attirer des conspécifiques mais aussi des hétérospécifiques autour du danger. Une association entre saison de reproduction et intensité du harcèlement a été rapportée chez un grand nombre d'espèces à échelle intraspécifique. La réponse aux appels hétérospécifiques varie-t-elle en fonction de la saison ?

Objectif :

L'objectif de cette étude est de déterminer si la réponse aux cris de harcèlement hétérospécifiques (sittelle et troglodyte) varie en fonction de la saison chez deux espèces de mésanges (charbonnière et bleue).

Résultats :

- les mésanges répondent plus aux cris de harcèlement à l'automne qu'au printemps, quelle que soit l'espèce émettrice.
- les mésanges répondent plus aux cris de la sittelle qu'à ceux du troglodyte, quelle que soit la saison.

Conclusion :

La saison influence la réponse des mésanges aux cris harcèlement. La réponse aux signaux hétérospécifiques pourrait être influencée par la prévalence des espèces dans les regroupements hétérospécifiques, la similarité acoustique ou encore l'apprentissage entre les espèces vivant dans les mêmes milieux.

Seasonal variation in mobbing behaviour of passerine birds

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Abstract

When they detect a predator, many birds exhibit mobbing behaviour and produce mobbing calls that quickly draw other preys against the predator. Such antipredator strategy often involves several species and imply thus heterospecific communication. Because fledging and nestling stages could be particularly targeted by predators a high mobbing intensity could be expected during the breeding season. While recognizing other species' mobbing calls is critical to set up this behavior, to date, we have no information about the perception of these calls according to the season. Here, we used playbacks of mobbing calls to study the variation in response of the Great Tit (*Parus major*) and the Blue Tit (*Cyanistes caeruleus*) exposed to mobbing calls of two heterospecific species, the Eurasian Nuthatch (*Sitta europaea*), and the Eurasian Wren (*Troglodytes troglodytes*). To investigate mobbing response seasonality, we conducted playback experiments during spring (breeding season) and autumn (non-breeding season). Contrary to most previous studies, we found that mobbing intensity was greater in autumn than in spring. Additionally, although neither Nuthatch nor Wren were related to Tit family, we found that both Tits species responded more to the former than the later species. At the heterospecific communication level, this study demonstrates a previously unsuspected level of complexity in the use of mobbing calls.

Keywords: Bird calls, Interspecific recognition, Interspecific communication, Mobbing, Passerines, Paridae

INTRODUCTION

The key role of anti-predation defenses in predator-prey relationships has been studied for many years, particularly for birds. When birds encounter predators, many species are likely to emit alarm calls. These alarm calls may be used to alert conspecifics of potential danger (Weary and Kramer 1995) or recruit nearby individuals for mobbing defense against the predator (Curio et al. 1978). Mobbing calls typically incite other potential prey to fly toward the caller and the predator. This mobbing behaviour may have several different functions and one of the most important is probably to drive the predator out from the vicinity (Pettifor 1990; Flasskamp 1994). The greater the number of mobbers, the greater the chances of driving away a predator (Krams et al. 2009; Picman et al. 1988). However, mobbing entails a real risk to the prey involved owing to its proximity to the predator (Denson 1979; Curio and Regelmann 1986). Preys adjust the strength of their mobbing behaviour according to the perceived risk associated to the predator's threat level (Billings et al. 2015; Dutour et al. 2016; Dutour et al. 2017a). Other factors including the proximity of the predator (Creswell 1993; Kleindorfer et al. 2005), its posture (Hamerstrom 1957; Coss and Ramakrishnan 2000) and its behaviour (Lind et al. 2005; Nolen and Lucas 2009) are also involved to explain the strength of the mobbing. Among these, seasonality is a probably important factor to explain mobbing behavior intensity.

Although mobbing can occurs in autumn and winter months, many studies have documented that the mobbing response to predator was higher during the breeding season (Altmann 1956; Shedd 1982; Shedd 1983; Krams and Krama 2002). Authors suggested that the willingness of birds to mob during the breeding season probably stems from at least two factors: (1) birds are territorial at this time and lack the option of easy relocation away from predators on their territories, and (2) birds are likely to have eggs or young more vulnerable to the predator (Shedd 1982). Some studies have also documented a temporal intensification in mobbing behavior during the breeding cycle. For example, parents increased the strength of the mobbing during the breeding cycle, whereas mobbing was probably rarely performed during nest building or egg-laying phase (Montgomerie and Weatherhead 1988; Redondo 1989). Finally, response intensity of individual to the mobbing playback was a significant predictor of reproductive success (Doran et al. 2005), although one study showed that mobbing calls can increase the rates of nest predation and lower breeding success (Krams et al. 2007). However, Dutour et al. (2017a) observed a reverse pattern when studying response at the birds' communities to Eurasian Pygmy Owl (*Glaucidium passerinum*), with a higher response rate in autumn than during the breeding season. Because study of Dutour et al.

(2017a) focused on a global response from all the species strongly predated to Pygmy Owl, any comparison across species remains possible. In addition, such experimental design does not allow to discriminate responses emitted toward predator from responses to interspecific mobbing calls. To our knowledge, the mobbing behaviour set up in response of interspecific calls have never been studied across seasons. Hence, there is a need for a pairwise comparison of caller-receiver species to explain their behavioural responses during different seasons.

Like other members of the Paridae family, the Great Tit (*Parus major*) and the Blue Tit (*Cyanistes caeruleus*) are highly vigilant and aggressive during mobbing events: they formed mixed-species flocks and mobbed together (Dutour et al. 2017a). Theses interspecific flocks can constitute facilitators of mobbing (Goodale and Kotagama 2005; Nolen and Lucas 2009). Here, we address one previously unexamined aspect of the mobbing behaviour of passerine birds. Indeed, we examine to what extent response to interspecific mobbing calls vary according to the season. We investigate the variation in response of the Great Tit and the Blue Tit exposed to the mobbing calls of the Eurasian Nuthatch (*Sitta europaea*) and the Eurasian Wren (*Troglodytes troglodytes*). We predicted that mobbing response should be more important during the autumn than during spring.

METHODS

Species and sites studied

The study was conducted in large mixed deciduous-coniferous forests near Lyon in Rhône-Alpes region (France; 45°80'N, 4°52'E). To ensure independence of experimental tests (no bird was tested twice during our study), playback sites were separated by more than 100 m and we never came back a second time on the same place. In addition, we avoided any temporal effect during our experiments by evenly distributed the playbacks of the different species across the study period. All tests were conducted in breeding season (April-Jun 2016) and in autumn (September-October 2016). Tests involved 140 different individuals (the detailed number of tests conducted for each combination was presented Table 1).

Playback Experiments

Once a focal bird was identified, we placed the loudspeaker used to broadcast the acoustic signal 30 m away from the bird at the base of a tree. We performed our playback experiments only when no other passerines were observed near the focus individual, to be sure that the response of the tested bird was due to our playback rather than to the behaviour of other passerines. All the tests for which an untargeted bird started to mob before the focal bird were discarded from the dataset. Once the loudspeaker was positioned, two observers with binoculars were stood opposite each other at vantage points beyond 15 m from the loudspeaker to observe bird response during the test. Test was divided into a 1 min baseline of silence followed by 1 min of signal playback. We found no evidence that our work disturbed the behaviour of the focal individual before the playback emission. During the playback, we considered that the focal bird responded positively to our test if it approached within a 15m radius of the loudspeaker (see Dutour et al. 2017b for more details).

Table 1 Details number of tests conducted for each combination in this study (*n* = 140)

		Playbacks			
		Nuthatch		Wren	
		Breeding season	Autumn	Breeding season	Autumn
Tested species	Blue Tit	15	21	15	15
	Great Tit	15	21	18	20

Choice of experimental stimuli and playback materials

The mobbing calls produced by Wren and Nuthatch in response to a pygmy owl or uploaded from Xeno Canto (XC file hereafter) online database were played with a Shopinnov 20W loudspeaker (frequency response 100Hz-15kHz). To limit pseudo replication (Hurlbert 1984; Kroodsma 2001), we used mobbing calls from 5 source individuals for the Wren (XC252499) and, for Nuthatch, we used two soundtracks recorded in two populations (Germany XC252502 and Sweden XC28224).

Statistical analysis

Analyses were done in R v.2.15.1 (R Development Core Team 2012). We used generalized linear mixed models (GLMM) to investigate the variation in mobbing propensity (i.e. speaker approach) among the receiver species (i.e. Great Tit or Blue Tit) and according to the mobbing stimuli broadcast (i.e. mobbing calls of Nuthatch and Wren) and the season (breeding season and autumn). More specifically, the individual binary response (mobbing response = 1; no mobbing response = 0) was introduced as dependent variable using a logit link and a binomial distribution for the error term, and the season, the receiver species, the mobbing stimuli and their interactive effect were introduced as explanatory terms in the fixed part of the model. Because different playback soundtracks were used for each receiver species, soundtracks were introduced in the model as random effects. We also performed model for each receiver species to investigate the variation in mobbing propensity according to the season and the mobbing stimuli.

RESULTS

Our analyses showed that the season, the receiver species and mobbing stimuli have a significant additive effect on the proportion of individuals which exhibited mobbing behaviour (Table 2; Fig. 1). Blue Tits responded stronger than Great Tits ($p = 0.033$). In Great Tits, both mobbing stimuli and season had a significant additive effect on the proportion of individuals which exhibited mobbing behaviour (season effect: $\chi_1^2 = 3.527$, $p = 0.060$; mobbing stimuli effect: $\chi_1^2 = 5.10$; $p = 0.024$). Great Tits mobbed 1.8 times more during autumn than they did during the breeding season. In response to Nuthatch calls, Great Tits were more likely to approach within 15 m of the loudspeaker than in response to Wren calls. Concerning the Blue Tits, we obtained the same result (season effect: $\chi_1^2 = 5.36$, $p = 0.021$; mobbing stimuli effect: $\chi_1^2 = 5.12$, $p = 0.023$): individuals mobbed 1.7 times more during the autumn than they did during the breeding season and were more prone to respond to Nuthatch calls than to Wren calls.

Table 2 Generalized linear mixed model type II Wald Chi-square results

Explanatory terms in the fixed part of the models	$\chi2$	*p*
season	9.65[a]	0.002
receiver species	4.521[a]	0.033
mobbing stimuli	9.236[a]	0.002
season*receiver species	0.229[a]	0.632
season*mobbing stimuli	0.036[a]	0.849
receiver species*mobbing stimuli	0.011[a]	0.915
season*receiver species*mobbing stimuli	0.593[a]	0.441

[a] *df* = 1

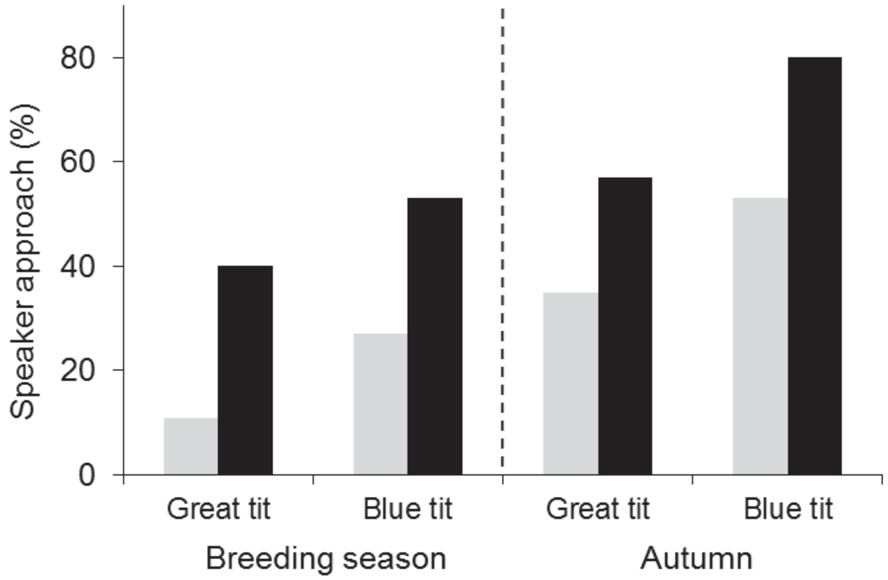

Fig. 1 Percentage of trials in which Great Tits and Blue Tits approached within 15 m of the loudspeaker during the presentations of mobbing calls of a Wren (grey) and a Nuthatch (black) in breeding season and autumn

DISCUSSION

Our playback experiments indicated that mobbing intensity was significantly greater in autumn than in the breeding season whatever the receiver species or the mobbing stimuli used and despite the fact that we may have tested juveniles (3-4 months old) with lesser experience on mixed-flocks and potentially showing weaker response. This result does not agree with most of the previous studies which have suggested an increased mobbing activity during the breeding season (e.g., Altmann 1956; Shedd 1982; Shedd 1983; Krams and Krama 2002). However, those studies examined mobbing behaviour in response to conspecific mobbing calls or to predator playbacks but not against interspecific mobbing calls (but see Tremblay and St Clair 2009). Nonetheless, these results confirm on the species scale the results obtained in a previous study conducted on the scale of the community (Dutour et al. 2017a). An increased mobbing activity during autumn could be explained by a seasonal variation of predators' diet, as predation pressure on passerine birds is probably different across seasons (Dutour et al. 2017a). In the case where birds make up a large share in the diet of the predator year round, vigorously attacking them at any time may make evolutionary sense (Cully and Ligon 1986; Nijman 2004; Chiver et al. 2017; Dutour et al. 2017a). In our case, a higher predation pressure in autumn could then explain more intense mobbing behaviors at this season. In addition, contrarily to the breeding season where the mobbing behaviour is constrained by territory boundaries (Betts et al. 2005), during the non-breeding season mobbing could occur in areas outside territory, increasing opportunities to respond to mobbing calls. Alternatively, higher mobbing intensity during autumn could be explained by migratory patterns. In the case birds tested are migratory birds; opportunities to meet local predators are lower, possibly leading Tits to respond to the mobbing calls of resident species in order to gather information (Nocera et al. 2008). Ultimately, an increased mobbing activity during autumn could be related to variations in sensitivity of the receiver (Lucas et al. 2002; Lucas et al. 2007). Indeed, during the breeding season, Tits spent time with their conspecifics (mate and nestlings) whereas they formed mixed-species flocks during the non-during season. We could suggest that species were more sensitive (i) to conspecific mobbing calls during the breeding season and (ii) to heterospecific mobbing calls during the non breeding season. During the breeding season, a focal individual have interest in responding to conspecific mobbing calls because the probability that mobbing calls were emitted by its mate was high, even though this strategy presumes individual recognition (Kennedy et al. 2009; Wheatcroft and Price 2008; McDonald 2012). Furthermore, for conspecifics, mobbing could play important indirect roles during the breeding season. For instance, da Cunha et al. (2017) suggest that males may use mobbing to display their phenotypic quality to females. In this case, predator mobbing could be seen as a way to influence sexual selection. Conversely, during the autumn and winter months, some passerine birds conduct the majority of their daily activities with mixed-species flocks (Ekman 1989). As birds often respond “by contagion” to the reactions of other birds, it is possible that during this period a higher number of prey species increase the propensity of birds to react and thus increase the strength of the mobbing as it has been shown by Sieving et al. (2004). Thus, in the non-breeding season, all these factors together can trigger a strong response of passerines to the mobbing calls of other species.

Our results indicated that Great and Blue Tits responded more strongly to the calls of Nuthatch and much weaker to those of Wren. The similarity in responses of Blue Tits and Great Tits to both Nuthatch and Wren calls suggests that they may use these signals in analogous manner. Nuthatch is a passerine which may occur in mixed flocks with Tits during the non-breeding season (Hinde 1952), whereas the Eurasian Wren is a species with which they do rarely co-occur. Thus, Tits may have opportunities to learn to associate heterospecific mobbing calls of Nuthatch with predatory threats, and this may contribute to the rapid spread of anti-predator behaviour within a bird community (Wheatcroft and Price 2013; Magrath et al. 2015; Suzuki 2016). Our results extend beyond simple learning as they suggest that previous exposure and learning maintain heterospecific responses (Wheatcroft and Price

2013), in addition to innate processes (Randler 2012; Dutour et al. 2017b). To test the role of learning between species, we could have considered to test juveniles with lesser experience on mixed-flocks in Autumn. Juveniles should respond weaker than adults. Other hypotheses could be advanced to explain an increasing mobbing response to Nuthatch: Tits are very similar in size to Nuthatches, occupy many of the same habitats, and are therefore attacked by most of the same predators. Furthermore, it has been found that White-Breasted Nuthatch (*Sitta carolinensis*), a close relative of Eurasian Nuthatch, had (i) a greater ability to detect the predator playback (Lucas et al. 2002; Lucas et al. 2007) and (ii) a greater tendency to mob before other species (Nolen and Lucas 2009). In our case, Eurasian Nuthatch may play a key role in the initiation of mobbing behaviour and it can be beneficial to respond to its mobbing calls. Tits make complex antipredator responses according to mobber's identity and their ecological relations. Recognizing other species' mobbing calls is critical for the efficiency of the antipredator behaviour. Previous study indicated that Red-Breasted Nuthatches (*Sitta canadensis*) discriminate between subtle differences in Black-Capped Chickadees (*Poecile atricapillus*) alarm calls that contain information about the size of potential predators (Templeton and Greene 2005; Templeton and Greene 2007). A next step is to study how passerine birds encode information about predator threat in their mobbing calls (see Carlson et al. 2017 for Paridae) and how this information is used by heterospecifics.

We have demonstrated that season influenced decision making in Tits. Overall, mobbing is a complex antipredator strategy, and a lot of parameters such as prevalence in flocks, similarity of mobbing calls or learning process among species sharing the same habitat may influence the expression of this behaviour. To continue research identifying mobbing and non-mobbing species will give information on species interdependence and avian community organization.

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Article 4 : Mobbing calls: a signal transcending species boundaries

Dutour, M., Léna, J.P., & Lengagne, T.
Animal Behaviour, 131 (2017), 3-11.

Problématique :

La reconnaissance des cris de harcèlement par les hétérospécifiques implique à première vue des processus d'apprentissage. Contrairement à la réponse innée, l'apprentissage associatif nécessite une expérience antérieure. Cependant, plusieurs processus non-appris comme la conservation phylogénétique ou la convergence structurelle des cris de harcèlement pourraient également jouer un rôle central dans la reconnaissance des cris de harcèlement hétérospécifiques.

Objectif :

L'objectif de cette étude est de démêler l'importance relative des différents mécanismes présentés ci-avant permettant la reconnaissance des cris de harcèlement hétérospécifiques en étudiant la variation de réponse de quatre espèces Européennes face à des cris de harcèlement inconnus (i.e. cris allopatriques) émis par trois espèces Américaines, limitant ainsi la part jouée par l'apprentissage.

Résultats :

- les cris de harcèlement de la mésange charbonnière sont proches de ceux des trois espèces allopatriques testées, auxquelles elle a répondu.
- les cris du pinson sont dissimilaires des cris allopatriques auxquels il n'a pas répondu.
- les cris de la mésange noire sont dissimilaires des cris allopatriques auxquels elle a globalement bien répondu.
- la mésange bleue répond plus aux cris de harcèlement des espèces avec lesquelles elle présente des dissimilarités.

Conclusion :

Les passereaux européens sont capables de répondre aux signaux allopatriques. La similitude acoustique ne semble pas être un mécanisme général permettant d'expliquer la réponse aux cris de harcèlement allopatriques.

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Mobbing calls: a signal transcending species boundaries

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When they detect a predator, some prey exhibit mobbing behaviour and produce mobbing calls that quickly draw a mixed conspecific and heterospecific group against the predator. While the efficiency of this strategy is often linked to interspecific communication, it raises the question of how animals recognize these signals as mobbing calls. It is usually suggested that associative learning about a predator when heterospecific mobbing calls are heard plays a crucial role in communication among species. Alternatively, phylogenetic conservation or evolutionary convergence could also explain this communication process. To determine whether prior experience is required to express a mobbing response, we conducted playback experiments with four European passerine species: great tit, *Parus major*, blue tit, *Cyanistes caeruleus*, coal tit, *Periparus ater*, and common chaffinch, *Fringilla coelebs*. The aim of the study was to examine whether they would respond to the mobbing signals of several North American passerines. As expected, because natural selection might shape a strong response to conspecific mobbing calls, our focal species reacted more strongly towards their own mobbing calls than towards those of American species. Nevertheless, for the three European species of tit, prior experience of heterospecific mobbing calls was not required to elicit a response. Additionally, for great tit and chaffinch, we found that acoustic similarity could explain behavioural responses to allopatric species. In contrast, such similarity was probably not the main mechanism underlying the response for the other two European species. Heterospecific response to mobbing calls probably involved many different mechanisms. Further studies focusing on each of these should allow us to understand their relative contribution to heterospecific communication.

When they perceive a potential predator, many species of birds and mammals produce specific alarm calls (Graw & Manser, 2007; Klump & Shalter, 1984; Magrath, Pitcher, & Gardner, 2007; Rainey, Zuberbühler, & Slater, 2004; Seyfarth, Cheney, & Marler, 1980). These calls are often classified as flee alarm calls, which are associated with the caller escaping while spurring other individuals to freeze or flee, or mobbing calls, which are associated with the caller approaching and harassing the predator while encouraging others to join it (Curio, 1978; Hartley, 1950; Hurd, 1996; Kennedy, Evans, & McDonald, 2009; Magrath, Haff, Fallow, & Radford, 2015). Mobbing calls are usually directed at an apparently nonhunting predator, and are expected to decrease its hunting efficiency, either by distracting it or by chasing it away (Curio, 1978; Flasskamp, 1994; Hoogland & Sherman, 1976; Pavey & Smyth, 1998; Pettifor, 1990). Both the intensity of mobbing and its success in deterring the predator are positively related to the size of the group gathered by the caller (Becker, 1984; Picman, Leonard, & Horn, 1988; Robinson, 1985; Verbeek, 1985). Although mobs can be formed exclusively by conspecifics, they often involve heterospecific prey (Dutour, Lena, & Lengagne, 2017; Hurd, 1996; Suzuki, 2016). Hence, this phenomenon makes mobs well suited for investigating communication at the community level. Indeed, as it implies a cooperative act, i.e. joining the mob, this makes it easier to distinguish between ‘simple’ eavesdropping on heterospecific signals and more elaborate interspecific communication. For instance, while some species will take part in the mob, others will not, although they perceive the same threat (Davies & Welbergen, 2009; Ito & Mori, 2010). As for other alarm calls, mobbing calls require the ability to gather relevant information from heterospecific signals (i.e. interceptive eavesdropping, sensu Peake, 2005; see Magrath et al., 2015 for a review), especially to recognize heterospecific mobbing calls.

Both learned and innate processes could be involved in the mechanisms enabling the recognition of heterospecific mobbing calls (Fallow, Gardner, & Magrath, 2011; Hurd, 1996; Magrath,

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Pitcher, & Gardner, 2009; Ramakrishnan & Coss, 2000; Wheatcroft & Price, 2013). By nature, associative learning is more flexible than innate processes but it requires previous experience to take place. Such experience could occur when heterospecific prey encounter each other when detecting and mobbing the same predator. However, several innate processes could also play a central role in the recognition of heterospecific mobbing calls. As for other alarm calls, there are strong ecological constraints on the acoustic structure of mobbing calls to increase their efficiency. Loudness and repeated features can be expected to be selected to facilitate locating the caller (Bradbury and Vehrencamp, 2011; Ficken & Popp, 1996; Jones & Hill, 2001; Klump & Shalter, 1984; Marler, 1955). Hence, these calls can also be used in other contexts that require accurate location of the caller such as maintaining contact with a partner or finding food (Mahurin & Freeberg, 2009; Marler, 1956; Suzuki, 2012). Moreover, calls inevitably incorporate some features such as harshness or broad bandwidth pulses of sound related to the psychological state of the caller, such as fright in the case of flee calls or arousal in the case of mobbing calls. All these characteristics can be expected to lead to acoustic similarity of mobbing calls across species, which could arise from phylogenetic conservation or evolutionary convergence of mobbing calls (Ficken & Popp, 1996; Johnson, McNaughton, Shelley, & Blumstein, 2004; Randler, 2012). Finally, both associative learning and innate processes could enhance recognition of heterospecific mobbing calls. Having similar acoustic features could greatly enhance the recognition of heterospecific mobbing calls through the mechanism of generalization which is often involved in the learning process (Sturdy, Bloomfield, Charrier, & Lee, 2007; Weary, 1991). Studies in some species of Paridae suggest that they learn to recognize their own mobbing calls and that they generalize to other unfamiliar calls that are acoustically similar.

Mechanisms involved in the recognition of heterospecific alarm and mobbing calls are still poorly understood despite heterospecific responses becoming well documented (Magrath et al., 2015). One way to fill this gap is to investigate the variation in response to unfamiliar alarm calls. Unfortunately, such data remain scarce in the case of mobbing calls. While in one study, individuals did not respond to the allopatric mobbing calls (Nocera, Taylor, & Ratcliffe, 2008), in others they did recognize them (Johnson et al., 2004; Langham, Contreras, & Sieving, 2006; Randler, 2012; Wheatcroft & Price, 2013). Because almost all studies have focused on one pairwise comparison of caller–receiver species, any comparison across species remains difficult, if not impossible. Moreover, in the studies on more than one caller–receiver pair, the heterospecific species responding to playbacks were not identified, preventing an understanding of responses in the light of the phylogeny. Hence, there is a need for a larger pairwise comparison of caller–receiver species to unravel the importance of the relationship among species to explain their behavioural responses in an antipredator strategy.

In this study, we conducted playback experiments to investigate the variation in response of four passerine birds exposed to the mobbing calls of three allopatric species. Additionally, we measured similarity among mobbing calls of the studied species to determine whether acoustic similarity could be viewed as a general mechanism involved in heterospecific communication. To test this, we played the calls of three North American passerine species to four European species, since mobbing is well documented in both communities and based on a similar alarm-calling system (Dutour, Lena, & Lengagne, 2016; Langham et al., 2006; Sieving, Hetrick, & Avery, 2010; Templeton & Greene, 2007). Then, as one study suggested a possible phylogenetically conserved response among the Paridae (Randler, 2012), we used sound tracks of three American species of Paridae: two corresponding to a mobbing call and one as a control (i.e. territorial call). Additionally, we chose to use a non-Paridae call to compare mobbing responses obtained from two different families.

METHODS

Study Species

The following European species were selected because they are known to exhibit mobbing behaviour when confronted with a predator and give specific mobbing calls: great tit, *Parus major*, blue tit, *Cyanistes caeruleus*, coal tit, *Periparus ater*, and common chaffinch, *Fringilla coelebs* (hereafter chaffinch; Thompson, 1969; Curio, 1971; Zimmermann & Curio, 1988; Krams & Krama, 2002; Lind, Jöngren, Nilsson, Schönberg Alm, & Strandmark, 2005; Berzins et al., 2010; Randler & Förschler, 2011; Randler & Vollmer, 2013; Dutour et al., 2016; Carlson, Healy, & Templeton, 2017). These European species were exposed to mobbing calls of three North American passerine species: black-capped chickadee, *Poecile atricapillus*, tufted titmouse, *Baeolophus bicolor*, and Carolina wren, *Thryothorus ludovicianus*. All of them are known to mob predators (Bartmess-LeVasseur, Branch, Browning, Owens, & Freeberg, 2010; Betts, Hadley, & Doran, 2005; Hetrick & Sieving, 2011; Hurd, 1996; Morton & Shalter, 1977; Sieving, Contreras, & Maute, 2004; Templeton & Greene, 2007; Templeton, Greene, & Davis, 2005). Tests involved 132 different European individuals (for the detailed number of tests conducted for each combination, see Table 1). Additionally, to ensure that the response was not due to call novelty (i.e. that the individuals did not simply respond to any novel sound) we used the territorial call of the boreal chickadee, *Poecile hudsonicus*, an American songbird found throughout Canada and the northern United States (Ficken, Mclaren, & Hailman, 1996), as a control (50 tests, see Table 1). Finally, to compare the relative intensity of mobbing responses to American species, we also broadcast conspecific mobbing calls to each of the four European species (44 tests, see Table 1).

Acoustic Analysis

Recordings were in 16-bit WAV format and analysed with Avisoft SASLab software (Avisoft Bioacoustics, Berlin, Germany). We used spectrograms with a fast Fourier transform length of 512 points for the measurements. We selected five recordings per species and analysed up to 10 songs per recording (on average 5.97 ± 2.43 SD). To properly characterize the mobbing calls of each species and to measure the variation across species, seven shared acoustic properties were measured on each call sound track: (1) duration (s); (2) peak frequency (the frequency for which amplitude (Hz) is maximum); (3) maximum frequency (highest frequency of the call in Hz); (4) minimum frequency (lowest frequency of the call in Hz); (5) frequency bandwidth (differences

Table 1
The number of tests conducted for each combination in this study

	Playbacks				
	Mobbing calls				Song
	Black-capped chickadee	Tufted titmouse	Carolina wren	Conspecific	Boreal chickadee
Coal tit	11	11	10	12	12
Blue tit	10	10	11	11	10
Great tit	13	10	10	10	15
Chaffinch	13	11	12	11	13

$N = 226$.

in Hz between maximum frequency and minimum frequency measure on a linear amplitude spectrum (threshold −20 dB)); (6) number of elements; (7) number of different elements per song, an indicator of call complexity (frequency modulated element or dee element or both, see Fig. 1).

Study Sites and Playback Experiments

All experiments were conducted on wild passerines inhabiting a large mixed deciduous–coniferous forest (ca. 570 km^2) located southeastern France (45°80′N, 4°52′). We never went back twice on the same forest path and two successive playbacks were always separated by more than 100 m (200 m for two tests performed on the same species). Hence although birds were not individually ringed, the probability of testing an individual twice was low. Moreover, all tests were conducted over a relatively short period during the breeding season (end of April to mid-July) to avoid a seasonal effect. In addition, we avoided any temporal effect during our experiments by evenly distributing the playbacks of the different species across the study period.

Once a focal bird was identified, we placed the loudspeaker used to broadcast the acoustic signal 30 m from the bird at the bottom of a tree. The focal subject was always the one nearest to the playback source. We performed our playbacks only when there were no other passerines observed near the focal individual that might have interfered with the test. All tests for which another bird mobbed before the focal one were discarded because we could not determine whether the focal individual responded to our playback test or to the mobbing call of the other bird. Two observers with binoculars were positioned opposite each other at vantage points at least 15 m from the loudspeaker and observed the bird's response during the test. To limit the risk of interference from nonfocal birds, we kept the test duration shorter than was usual in previous studies (including our own, Dutour et al., 2016; see also Randler & Vollmer, 2013). More precisely, each test was divided into a 1 min baseline of silence followed by playback of a signal containing a series of individual calls following a natural rhythm (1 min). We found no evidence that our arrival disturbed the behaviour of the focal individual before the playback. During the playback, focal birds either did not approach the loudspeaker (i.e. staying around 30 m from it) and continued their usual activity (i.e. singing, foraging or resting) or approached it within a 15 m radius. We therefore used this distance of approach to assess the mobbing propensity of focal birds as in Hua et al. (2016). A preliminary analysis confirmed that birds approaching the soundtrack within a 15 m radius were 20 times more likely to produce mobbing calls than those that did not approach it (95% confidence interval, CI: 21.75–59.15). Furthermore, approaching birds also exhibited other mobbing behaviours (circling the loudspeaker, restless movements), although these behaviours were not quantified. Neither the latency to approach (i.e. time of arrival) nor the closest approach (i.e. the minimal distance from the loudspeaker) were found to be related to the production of mobbing calls by approaching birds (see Appendix Table A1). Data on species identity and mobbing response of the focal birds were collected mainly by one observer (M.D.), and were supplemented by a second observer who recorded the birds' behaviour.

Choice of Experimental Stimuli and Playback Materials

In the field, the amplitude of mobbing calls of these species has not been measured accurately before (i.e. the precise distance between the bird and the sound level meter taking the exact position of the head of the bird into account). Hence, we decided to match by ear the amplitude of the calls used during our test to a natural call produced by passerines while mobbing. Then, the average amplitude used for the playback was obtained with a sound level meter placed 1 m from the loudspeaker (86.2 ± 3.07 dB, mean ± SD, Lutron SL-4001, C weighting, slow settings, re: 20 μ Pa). The same volume was used for all species. We broadcast sound tracks using a Shopinnov 20 W loudspeaker (frequency response 100 Hz–15 kHz) that included a memory to store the sound file.

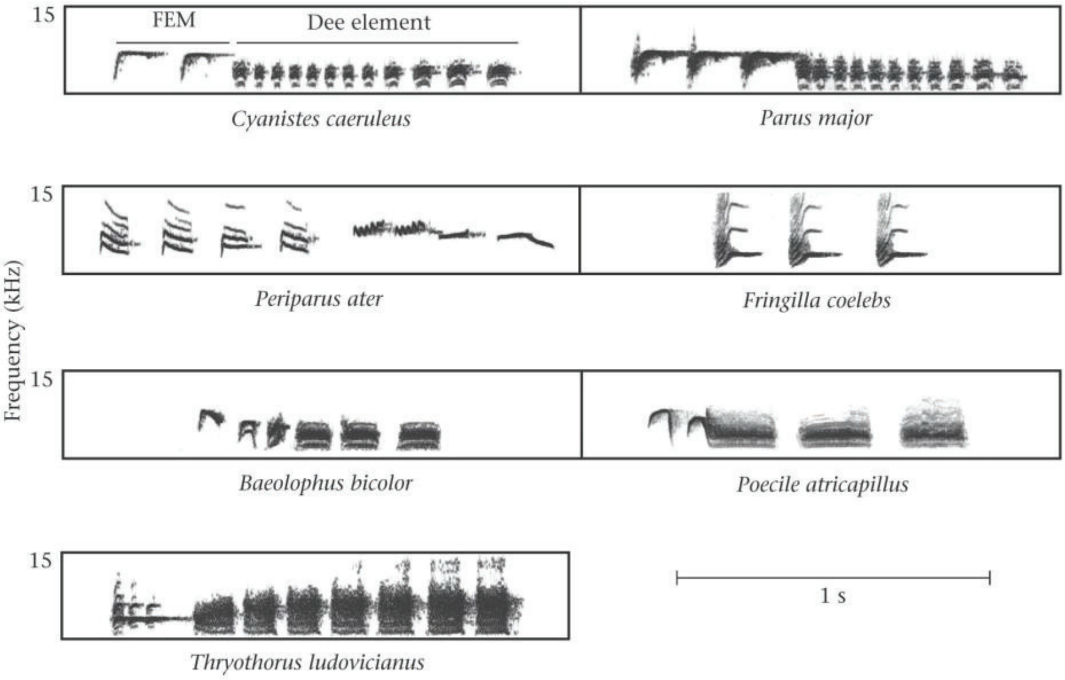

Figure 1. Spectrograms of the mobbing calls of the species studied. Spectrograms were produced with Avisoft SASLab (frequency sampling 44.1 kHz, FFT length 512 points). These calls are composed of different note types: frequency modulated element (FME; Lengagne, Lauga, & Aubin, 2001) or dee element ('D' notes or churr notes) or both. See text for further details of measurements.

For the playback, we used mobbing calls of passerines produced in response to a Eurasian pygmy owl, *Glaucidium passerinum*, and to conspecific mobbing calls. Calls were recorded with a Fostex FR2LE digital recorder connected to a Sennheiser ME67-K6P microphone. We also used mobbing calls obtained from the Macaulay Library (Cornell Lab of Ornithology, http://macaulaylibrary.org) or from the Xeno Canto online database (www.xeno-canto.org). To avoid pseudoreplication (Hurlbert, 1984; Kroodsma, 1989, 1990), calls from 40 individuals were used (five from each species). Each stimulus was played back at the same volume to copy natural calling amplitudes.

Statistical Analyses

To compare the acoustic similarity of calls of European and North American species, we carried out four principal components analyses (PCA) using acoustic measurements taken from mobbing calls of the seven species (Fig. 1). These four PCAs included peak frequency, minimum frequency, frequency bandwidth, number of different elements and number of elements. The PCAs of great tit and blue tit also included duration. For the chaffinch and coal tit this acoustic measurement was excluded because it was strongly correlated with number of elements (chaffinch: $r^2 = 0.89$; coal tit: $r^2 = 0.86$; both $P < 0.001$). Maximum frequency was excluded for each of the four European species because it was strongly correlated with frequency bandwidth ($0.84 < r^2 < 0.99$, $P < 0.001$). Analyses were done in R v.2.15.1 (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org) using the ade4 package (Dray & Dufour, 2007).

Because none of the focal birds (regardless of species) mobbed when exposed to the novelty signal (i.e. the territorial call of the boreal chickadee; $N = 50$), it was not possible to include this experimental treatment in a parametric analysis. For each receiver species (i.e. the species to which we played the mobbing calls), therefore, we used a Fisher exact or chi-square homogeneity test to compare the mobbing propensity, as revealed by the relative frequency of mobbing birds, between the novelty signal and the other three heterospecific mobbing stimuli (black-capped chickadee, tufted titmouse and Carolina wren mobbing calls). For each receiver species, a similar test was also performed to compare the mobbing propensity between the novelty signal and the conspecific mobbing stimulus. We then used a generalized mixed model (GLMM) to investigate how the mobbing propensity varied between species and between the mobbing stimuli broadcast, thus discarding the novelty signal treatment from the analysis. More specifically, the individual binary response (mobbing response = 1; no mobbing response = 0) was introduced as the dependent variable using a logit link and a binomial distribution for the error term, and the receiver species, the mobbing stimuli and their interaction effect were introduced as explanatory terms in the fixed part of the model. Because five different playback soundtracks of each mobbing stimulus were used twice for each receiver species, soundtracks were introduced in the model as random effects. All coal tits mobbed when a conspecific mobbing call was played, resulting in aliasing between this explanatory term combination and a complete set of soundtrack random effects (i.e. the coal tit's mobbing calls). We therefore used the Laplace optimization method to circumvent the optimization problem and to allow a log-likelihood estimation of the model required to perform likelihood ratio tests (LRT). The significance of the random effect was tested using an LRT on the full model. We also used LRT to test the significance of explanatory terms, and removed nonsignificant explanatory terms to obtain the final model. We then performed an analysis of deviance to examine the relative importance of the variation explained by the heterospecific status of the stimuli. For this purpose, we constructed a concurrent but reduced model for which all heterospecific stimuli were regrouped within a unique category and compared to the conspecific one. An *F* statistic was then calculated to test the significance of the variation caught by this group. We used a similar approach to investigate whether the difference in response of receiver species to the conspecific and the heterospecific mobbing calls could be explained by their phylogenetic relationship at the family level (hereafter family origin). For this purpose, the mobbing stimuli were regrouped into two classes (heterospecific versus conspecific calls) and the receiver species were regrouped according to their family origin. Finally, we performed a separate analysis on the conspecific mobbing call treatment to control for variation in mobbing propensity according to the receiver species. We also performed a partial analysis for each receiver species to investigate the variation in mobbing propensity according to the mobbing stimuli using LRT-based contrasts. For both these analyses, the soundtrack random effect could not be estimated, reducing the models to generalized linear models (GLM). Analyses were done using SAS 9.3 software (SAS Institute Inc., Cary, NC, U.S.A.).

Ethical Note

All tested birds returned to normal activity relatively quickly after the playbacks (usually within 1 min), so we were confident that they were not unduly stressful. All behavioural observations performed during this study complied with the legal requirements in France and followed the ASAB/ABS Guidelines for the Use of Animals in Research. The study complied with the ethical rules set by University Lyon 1 concerning the use of wildlife species in research programmes. The study was conducted with the approval of the Prefecture du Rhône (Ref 2015-13).

RESULTS

Acoustic Similarity of Mobbing Calls

A PCA was performed on acoustic characteristics for each of the four European species to determine the similarity of their mobbing calls to those of allopatric species (Fig. 2). In two cases, chaffinch and coal tit, we observed a strong dissimilarity between the focal and allopatric species (Fig. 2a and b). For the great tit, PCA revealed an important overlapping with mobbing calls of the allopatric species (Fig. 2c). Finally, blue tit mobbing calls showed a strong similarity with those of the black-capped chickadee but no overlapping with mobbing calls of the Carolina wren and tufted titmouse (Fig. 2d).

Response to Mobbing Calls

As highlighted in the Methods, none of the European species responded to the novelty signal (i.e. the territorial call of the boreal chickadee). Nonparametric tests showed that all European species responded significantly less to the novelty signal than to conspecific mobbing calls (territorial call versus conspecific mobbing calls: great tit: $N = 25$, $P < 0.001$; blue tit: $N = 21$, $P = 0.001$; coal tit: $N = 24$, $P < 0.001$; chaffinch: $N = 24$, $P < 0.001$). Furthermore, our results showed that all three tit species responded significantly less to the novelty signal than to the mobbing calls of the American species (black-capped chickadee, tufted titmouse and Carolina wren pooled; territorial call versus. mobbing calls: great tit: $N = 48$, $P < 0.001$; blue tit: $N = 41$, $P = 0.002$; coal tit: $N = 44$, $P = 0.009$). The chaffinch's response did not differ significantly between the novelty signal and mobbing calls ($N = 49$, $P = 0.167$). Responses to the novelty signal were thus discarded for the rest of the analyses.

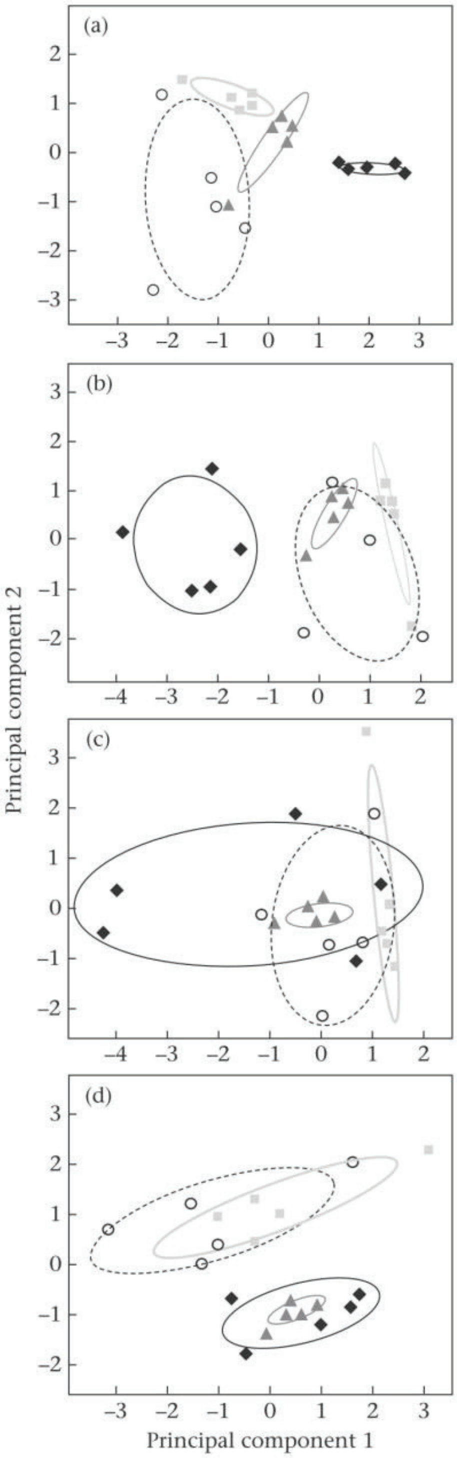

Figure 2. Principal components plots of the acoustic characteristics of European and North American birds' mobbing calls. European birds (◆): (a) chaffinch (PC1: 40.9%; PC2: 23.2%), (b) coal tit (PC1: 50.3%; PC2: 22.3%), (c) great tit (PC1: 40.1%; PC2: 26.5%) and (d) blue tit (PC1: 33.2%; PC2: 21.9%). North American birds: tufted titmouse (■), black-capped chickadee (▲) and Carolina wren (○). The contour lines indicate the 68% probability of belonging to each putative cluster (i.e. species) which can be used to examine graphically the similarity between species. See Appendix Table A2 for pairwise comparisons performed separately on PC1 and PC2 between European and North American mobbing calls.

According to the GLMM used to analyse the variation in the receiver species' responses and in the different mobbing signals, we detected a significant soundtrack random effect ($\chi^2_{3.60} = 3.60$, $P = 0.03$; see Table 2). The pattern of responses to the different mobbing signals also varied significantly between the receiver species, as indicated by a significant interaction effect between the receiver species and the mobbing signals ($\chi^2_{18.92} = 18.92$, $P = 0.03$; see Table 2). As revealed by a deviance analysis, a significant part of this interaction effect could be explained by the variation between the receiver species in the relative response difference between heterospecific and conspecific mobbing calls ($F_{7,8} = 4.04$, $P = 0.03$; see Table 2 for details). Although all species responded to conspecific mobbing calls (see partial analysis below), the relative strength of this response when compared to all pooled heterospecific calls varied significantly across receiver species (Fig. 3). Furthermore, this variation in response between the conspecific and the heterospecific calls observed in the receiver species was at least partly explained by their family origin ($F_{3,12} = 5.42$, $P = 0.01$; see Table 2 for details). The chaffinch showed a higher response to conspecific than heterospecific mobbing calls, regardless of species, while this difference was relatively less and more heterogeneous within the tit species (Fig. 3, Table 3). Partial analysis of the response towards conspecific mobbing calls did not indicate a significant variation in mobbing propensity between species ($\chi^2_{6.93} = 6.93$, $P = 0.074$), although the response of the coal tit was stronger than that of the other three species. Separate analyses performed for each receiver species indicate that both coal tit and chaffinch were significantly more prone to respond to conspecific calls than to heterospecific ones while this was not the case for the great tit and the blue tit (see Table 3, Fig. 3). In contrast to the great tit and the chaffinch, both the blue tit and the coal tit exhibited some variation in their response towards the three different heterospecific calls, although these variations were not statistically significant (see Table 3, Fig. 3).

DISCUSSION

We found that European birds responded selectively to the broadcast of mobbing calls of North American passerines but not

Table 2
Deviance and AIC according to the terms introduced in the fixed part of the generalized mixed model

Explanatory terms in the fixed part of the models	N_p	Deviance	AIC
Receiver | C(conspecific versus heterospecific)	8	196.09	214.09
R(tits versus chaffinch) | C(conspecific versus heterospecific)	4	206.36	216.36
R(tits versus chaffinch)+C(conspecific versus heterospecific)	3	208.53	216.53
R(tits versus chaffinch) | Caller	8	199.03	217.03
Receiver | Caller	16	185.66	219.66
Receiver+C(conspecific versus heterospecific)	5	207.94	219.94
Receiver+Caller	7	204.58	220.58
Receiver	4	218.41	228.41
Caller	4	220.23	230.23
Intercept	1	235.32	239.32

The « | » character indicates the addition and interaction between the explanatory terms. Receiver: four receiver species; caller: four mobbing call stimuli, R(tits versus chaffinch): receivers species grouped into two class according to the family of origin; E(conspecific versus heterospecific): mobbing call stimuli grouped into two classes, heterospecific versus conspecific calls. N_p: number of parameters in the fixed part of the model; AIC: Akaike's information criterion. The significance of explanatory terms was tested using a likelihood ratio test or an F test in the case of constrained structures for the receiver or the caller effect (see main text). For all models, the playback soundtrack of each mobbing stimulus was a random factor in the response. $N = 176$.

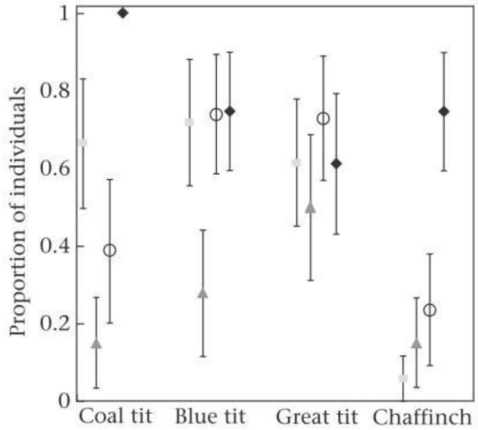

Figure 3. Proportion of European birds responding to the presentations of mobbing calls of a tufted titmouse (■), a black-capped chickadee (▲), a Carolina wren (○) and a conspecific (◆). Error bars represent SEs. See Appendix Table A3 for detail pairwise comparisons of responses between all mobbing call stimuli for each receiver species.

Table 3
Overall difference in responses between birds exposed to heterospecific and conspecific calls, and overall difference in responses between birds exposed to different heterospecific calls

Comparison	Receiver species	*df*	χ^2	*P*
Conspecific versus heterospecific calls	Blue tit	3	5.6	0.13
	Coal tit	3	21.86	<0.0001
	Great tit	3	0.85	0.84
	Chaffinch	3	13.38	0.004
Difference between heterospecific calls	Blue tit	2	4.84	0.09
	Coal tit	2	4.92	0.09
	Great tit	2	0.85	0.65
	Chaffinch	2	1.46	0.48

All comparisons were based on a partial analysis for each receiver species using an LRT-based contrast. See Appendix Table A3 for details of pairwise comparisons of responses between all mobbing call stimuli for each receiver species.

to the boreal chickadee territorial call, which is usually directed at conspecifics, whereas the mobbing calls are addressed to both conspecifics and heterospecifics. These results corroborate the study of Randler (2012) showing that great tits responded more strongly towards allopatric chick-a-dee mobbing calls than towards the allopatric territorial call. In that study, 31.3% of individuals (five of 16) approached the loudspeaker during the black-capped chickadee territorial call playback, while during our playback of boreal chickadee territorial calls, none of 50 individuals mobbed the loudspeaker. Unlike us, Randler started the trials at the beginning of the territorial phase of great tits (Hölzinger, 1997). The stronger response to an allopatric territorial call at the beginning of the territorial phase could be explained by great tits modifying the mobbing response according to the stage of breeding.

Our results clearly show that for three of the four species tested, that is, the three species of tit, prior experience of the heterospecific mobbing call was not required to elicit a response. Moreover, American mobbing call playbacks elicited mobbing responses from nine other bird species, including different genera, such as *Troglodytes*, *Regulus*, *Sitta*, *Lophophanes*, *Poecile*, *Turdus* and *Garrulus*. Natural selection might be expected to favour the strongest response to a species' own mobbing calls. Indeed, European passerines reacted more strongly towards European conspecific mobbing calls than those of North American species. Nevertheless, focusing on differences between species, we found large variation in their behavioural response. In particular, the propensity of the chaffinch to respond to heterospecific mobbing calls was clearly lower than that found for the three tit species. Furthermore, although tits responded well to heterospecific mobbing calls, to some extent their responses remained heterogeneous. Like the chaffinch, the coal tit responded less to the allopatric calls than the conspecific calls. Therefore, these results strongly suggest variability between species, which could well explain differences between previous studies (Johnson et al., 2004; Nocera et al., 2008; Randler, 2012).

Three hypotheses, not mutually exclusive, could be suggested to explain the responses to unfamiliar mobbing calls: (1) phylogenetic conservation of the signal structure; (2) evolutionary convergence due to similar constraints on the signal structure; and (3) acoustic communication system complexity.

First, several studies suggest phylogenetic relatedness affects existing sensory bias in the receiver and the structure of calls (De Kort & ten Cate, 2001; Ryan, 1998; Ryan & Rand, 1993). Calls of different species can be acoustically similar if calls retain features of their acoustic structure from a common ancestor (De Kort & ten Cate, 2001), thus enabling interspecific responses among related species. This hypothesis could well explain the response of the chaffinch to allopatric mobbing calls we observed in our study, since none of the calls we used came from species in the chaffinch's own family. The response of the European tit species to the American tit species could also be due to the highly conserved call structure of the Paridae throughout the Holarctic (Langham et al., 2006; Randler, 2012). In agreement with the study conducted by Randler (2012) suggesting that the response of the great tit to allopatric mobbing calls could be phylogenetically conserved, we observed in the present study a strong overlapping between characteristics of mobbing calls produced by this species and by the three allopatric species. Surprisingly, all three tit species responded as strongly to the Carolina wren mobbing call as to the mobbing calls of the two tit species. Hence, the difference in response across the heterospecific mobbing calls may not be explained by the species being in the same family.

The second mechanism to explain the responses observed to allopatric mobbing calls could be evolutionary convergence of the acoustic features (Johnson et al., 2004). To facilitate locating the calling bird and recruitment for mobbing, acoustic signals frequently contain repeated calls, strongly modulated in amplitude, with a large frequency band and produced with high amplitude (Aubin & Jouventin, 2002; Bradbury and Vehrencamp, 2011; Brown, 1982; Marler, 1955). In the same way, many studies suggest that flee alarm calls produced by several species share the same acoustic structures so that the birds are not located by the predator while calling (Brown, 1982; Jones & Hill, 2001; Shalter, 1978). The strong selective pressure imposed by predators on the communication process (being located in the case of mobbing calls or not located in the case of flee alarm calls) may lead many species to share the same acoustic structures and could at least partially explain heterospecific communication (Bradbury and Vehrencamp, 2011; Fallow et al., 2011; Johnson et al., 2004; Marler, 1955). Previous studies suggest that both acoustic similarity and learning are important for interspecific responses to alarm calls (Fallow et al., 2011; Haff & Magrath, 2012). In the present study, the fact that three of four European species responded to mobbing by allopatric American species suggests that acoustic structure similarities could explain our results (Fallow et al., 2011). Nevertheless, our acoustic analysis revealed differences between species (Fig. 2). Acoustic similarity could explain the behavioural response to allopatric species in both the chaffinch (strong acoustic differences with the allopatric call and weak behavioural responses) and the great tit (strong acoustic similarities and strong behavioural responses to allopatric species). Great tits responded to calls that were acoustically similar to their own. This suggests that they generalize responses from conspecific calls to unfamiliar calls that are acoustically similar (Ghirlanda & Enquist, 2003). Indeed, if a great tit learns to recognize its own mobbing calls, then with generalized responding, any calls that it hears that are acoustically similar enough to its own would be treated as 'mobbing calls' (Sturdy et al., 2007; Weary, 1991). On the other hand, acoustic similarity did not explain the behavioural response to allopatric species in the coal tit (strong behavioural responses to the allopatric call despite strong acoustic differences with them) and the blue tit, although for this species the results are more complex (Figs 2d and 3). To sum up, similarity of the acoustic features seems not to be a universal hypothesis to explain our results as suggested by Wheatcroft and Price (2013).

A third hypothesis, dealing with acoustic communication system complexity, may explain why the three European tit species responded strongly to American mobbing calls while the chaffinch did not. Calls are structurally complex in tits and chickadees because of the presence of different elements (Suzuki, Wheatcroft, & Griesser, 2016), and responses can depend on the number of elements such as C or D notes (Freeberg & Lucas, 2002). Previous studies have suggested that mobbing calls contain information about the degree of threat that a predator represents (Baker & Becker, 2002; Hetrick & Sieving, 2011; Templeton et al., 2005). Parid species exhibit two very different signals in response to flying or perched predators. Finally, most of these species have rich territorial call repertoires. In contrast, the chaffinch calling system seems to be less structurally complex than that of tits and chickadees. For instance, the call rate is the most significant determinant of whether other birds interpret the vocalization as a mobbing call (Randler & Förschler, 2011). Therefore, the complexity of a bird's call structures, which is probably associated with its cognitive capacity to decode information, may explain the differences observed between the responses of European tits and chaffinches. Further studies focusing on species for which the mobbing system is based on a simple variation in call rate would be interesting to assess how birds might respond differently to heterospecifics.

In conclusion, our study has emphasized that prior experience is not a prerequisite for heterospecific communication. The allopatric response to mobbing calls of three American species by four European ones shows that a mobbing response could be obtained without these calls being learned. We found that for two of four species studied, acoustic similarity could explain their behavioural response to calls of allopatric species. Nevertheless, the complexity of the communication system in many passerine species probably prevents us finding a general phenomenon that can be applied to all species. For instance, in chickadee species, within a given mobbing call sequence, some elements involve early experience while others do not (Hughes, Nowicki, & Lohr, 1998). Further studies, including the use of different passerine species with different complexity levels of their communication system, are now necessary to assess differences in phylogenetic relationships, acoustic parameters and acoustic communication system complexity.

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APPENDIX

Table A1
Influence of the latency and the closest approach on the mobbing call propensity

Explanatory term	Numerator *df*	Residual *df*	*F*	*P*
Latency	1	60	0.04	0.847
Closest approach	1	60	0.05	0.824
Latency∗Closest approach	1	60	0.33	0.566

A logistic model was used to examine whether the latency (i.e. time of arrival within the 15 m radius around the loudspeaker) and the closest approach (i.e. the minimal distance from the loudspeaker) were related to the production of mobbing calls by approaching birds.

Table A2
Pairwise comparisons of the two principal components of the mobbing calls of European and North American birds

	Tufted titmouse		Black-capped chickadee		Carolina wren	
	PC1	PC2	PC1	PC2	PC1	PC2
Chaffinch	**0.008**	**0.008**	**0.008**	0.151	**0.008**	0.151
Coal tit	**0.008**	0.548	**0.008**	0.309	**0.008**	0.548
Great tit	**0.032**	0.548	0.841	0.690	0.548	0.548
Blue tit	0.548	**0.008**	0.690	0.841	0.095	**0.008**

PC1 and PC2: first and second principal components. All comparisons were done using a Wilcoxon exact test given the low sample size (i.e. $N = 10$ for each test) P values were not corrected for multiple comparisons. Significant P values are indicated in bold.

Table A3
Pairwise comparisons of responses to all mobbing call stimuli for each receiver species

Receiver species	Pairwise comparison	χ^2	P
Blue tit	Conspecific vs BC	0.02	0.89
	Conspecific vs CW	0	1
	Conspecific vs TT	3.96	0.04
	BC vs CW	0.02	0.89
	BC vs TT	3.29	0.07
	CW vs TT	3.96	0.04
Coal tit	Conspecific vs BC	6.83	0.009
	Conspecific vs CW	12.32	0.0004
	Conspecific vs TT	20.36	<0.0001
	BC vs CW	1.18	0.28
	BC vs TT	4.92	0.03
	CW vs TT	1.24	0.27
Great tit	Conspecific vs BC	0.01	0.94
	Conspecific vs CW	0.22	0.64
	Conspecific vs TT	0.2	0.65
	BC vs CW	0.18	0.67
	BC vs TT	0.31	0.58
	CW vs TT	0.84	0.36
Chaffinch	Conspecific vs BC	11.81	0.0006
	Conspecific vs CW	5.45	0.02
	Conspecific vs TT	6.99	0.008
	BC vs CW	1.44	0.23
	BC vs TT	0.6	0.44
	CW vs TT	0.16	0.69

All comparisons were based on a partial analysis for each receiver species using an LRT-based contrast. BC: black-capped chickadee; TT: tufted titmouse; CW: Carolina wren.

Article 5 : Relative divergence of mobbing calls and songs structures in passerine birds and the importance of acoustic features for localization efficiency

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Problématique :

Au cours des dernières décennies, beaucoup de travaux ont été réalisés sur le rôle de la divergence des signaux comme moteur de la spéciation. Cependant, dans certains cas, les signaux sont utilisés pour communiquer entre espèces. Ce type de communication bien particulier est-il rendu possible par un phénomène de convergence de certaines structures acoustiques ?

Objectifs :

Les deux principaux objectifs de cette étude sont de tester si la divergence ou la convergence des signaux acoustiques chez 23 espèces de passereaux varie selon (1) le support fonctionnel qui leur est associé (ici les cris de harcèlement *versus* les chants territoriaux) (2) les contraintes environnementales exercées sur la propagation le contexte environnemental, c'est-à-dire l'habitat fermé v*ersus* l'habitat semi-ouvert, et tenant en compte de l'inertie phylogénétique.

Résultats :

- les cris de harcèlement ont des largeurs de bande de fréquence plus grandes que les chants territoriaux.
- les cris de harcèlement sont globalement plus similaires entre eux que les chants territoriaux pour le paramètre clef associé à la fonction de localisation (largeur de bande de fréquence)
- les cris de harcèlement présentent un pic de fréquence plus élevé que les chants en milieu ouvert alors qu'il n'y a pas de différence en milieu fermé.

Conclusion :

Nos résultats suggèrent une évolution convergente sur la largeur de bande de fréquence des cris de harcèlement. La large bande de fréquence présente dans les cris de harcèlement de toutes les espèces indique que cette caractéristique acoustique est essentielle pour la communication lors du harcèlement. D'un point de vue psychoacoustique, ce type de structure permet une localisation rapide de l'émetteur, processus indispensable pour rameuter des proies potentielles dans le cadre du harcèlement.

Relative divergence of mobbing calls and songs structures in passerine birds and the importance of acoustic features for localization efficiency

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Abstract

Divergence and convergence in acoustic signals may be driven by deterministic (i.e. natural selection) or stochastic processes. Uncertainly about which of these factors best explains the patterns of acoustic variation between species has fuelled a long-standing debate in evolutionary biology. A selection process according to the functional supports of acoustic signals has been described. To compare the relative divergence of vocalizations according to their functional support, we examine two types of signals within 23 bird species living in different habitats: (i) mobbing calls emitted to recruit both conspecifics and heterospecifics against predator and require the sender to be easily localizable, and (ii) territorial songs, a signal playing an important role in sexual and social communication. In the present study, we demonstrate that divergence of acoustic features varies according to their functional support (mobbing calls versus territorial songs) and the environmental contrast. We found that the frequency band of mobbing calls overlaps among species, suggesting convergent evolution for this acoustic feature. Among habitat types, the peak frequency is higher for mobbing calls than territorial songs among species living in semi-open habitat, but not among forest species. Our results indicate a substantial within species variance for the two types of vocalization illustrating the importance of considering residual variance in analyses.

Keywords: acoustic signal divergence, passerine, birdsong, mobbing call, frequency bandwidth, acoustic communication, signal evolution

INTRODUCTION

In many animals, acoustic communication plays a central role in a variety of behavioral contexts such as mate selection, territorial defense, predator avoidance, group cohesion and foraging (Zuberbühler *et al*., 1997; Parks *et al*., 2014) Both temporal and/or spectral features of acoustic signals are used to transmit information from the emitter to the receiver although broad variations exist among taxa in their ability to produce complex signal features. These features are altered during propagation either through degradation, attenuation, or mixing with background noise in the environment. At last, information transfer efficiency depends on the receiver ability to detect and discriminate information in the perceived signals in spite of its alteration (Guilford & Dawkins 1991; Brémond & Aubin, 1992).

During the last decades, a large effort has been done to unravel the evolution of acoustic communication in different taxa and three main sources of acoustic divergence have been identified (Wilkins *et al*., 2013). Firstly, sexual selection has been rapidly recognized as a powerful evolutionary driver of acoustic signal divergence given their involvement in mate choice (Wilkins *et al*., 2013; Pearse *et al*., 2018). For instance, numerous studies showed the existence of characters displacement when closed species are in contact (Pfennig & Pfennig, 2010). Secondly, indirect environmental selection may affect traits that are also involved in the production and/or modulation of vocalization (i.e. pleiotropic effect). Indeed, ecological selection may apply on some morphologic traits such as body size (and beak size/shape in birds), resulting in indirect selective effect on acoustic signals since these traits are also involved in acoustic signal production. Lastly, both cultural and genetic drift can also drive acoustic divergence in the absence of selective pressure (Wilkins *et al*., 2013). For instance, in the greenish warblers (*Phylloscopus trochiloides*), spatial divergence in territorial calls is mainly related to the genetic distance but not to ecological divergence (Irwin *et al*., 2008). Such a neutral process is also expected to be more important in the case of complex acoustic signals and learning (Wilkins *et al*., 2013).

As outlined by Wilkins *et al*. (2013), all these evolutionary drivers are not mutually exclusive, and their interactive effect will also depend on the environmental constraints imposed on the transmission efficiency. Indeed, as first suggested by Chappuis (1971) and Morton (1975), birds living in forest may vocalize at a lower frequencies than species living in open habitat because lower frequencies are less degraded during propagation in closed habitats. These last years, this environmental constraint on sound propagation has been extensively examined in mating signal within different taxa and according to different environmental constraints (Ey & Fisher, 2009; Roca *et al*., 2016), especially in birds for which meta-analyses (Boncoraglio & Saino, 2007; Roca *et al*., 2016) and relatively large phylogenetic analyses (Derrybery *et al*., 2018, Pearse *et al*., 2018) are now available. All these studies suggest a moderate effect of habitat on birdsong divergence which is mainly associated to one spectral acoustic feature, the peak frequency (i.e. the frequency for which amplitude/energy is maximum) (Boncoraglio & Saino, 2007; Pearse *et al*., 2018). This relatively weak effect of environmental constraints on acoustic signal divergence could be explained by evolutionary trade-offs applying to the functional support of the studied acoustic signal (Boncoraglio & Saino, 2007; Ey & Fischer, 2009). For instance, in the case of mate selection, it is likely that emitters have to make a trade-off between the transmission efficiency needed to attract conspecific mates over long distance and the energetic cost as well as the risk of eavesdropping by predators or parasites in doing so (Eye & Fisher, 2009). Moreover, as demonstrated in the silvereyes (*Zosterops lateralis*), such an acoustic adjustment to environmental constraints could result from phenotypic plasticity, a phenomenon which could be widespread in bird response to anthropogenic environmental constraints (Potvin & Mulder, 2013).

Studying acoustic signals associated to other functional supports than mate selection or territorial defense may be particularly helpful to disentangle the relative contribution of each evolutionary driver as well as their interactive effect with environmental constraints (Ey & Fischer, 2009; Wilkins *et al*., 2013; Billings, 2018). In birds as in mammals, acoustic communication is also largely involved in other behavioral contexts, such as parent-offspring relationship or predatory avoidance (Lengagne *et al*., 1999a; Leavesley & Magrath, 2005). In the case of predator avoidance, two kinds of acoustic signal have been mainly documented, flee alarm calls and mobbing calls, and each are associated to a distinct and quite contrasted function (Marler, 1955; Magrath *et al*., 2015): flee alarm calls are emitted by escaping individuals and trigger freezing or fleeing in listeners. This functional support is associated to particular acoustic features, notably high frequency and slow rise times of the acoustic elements which make the sender hard to localize (Marler, 1955; Klump & Shalter, 1984; Klump, 1996). At the opposite, mobbing calls are emitted by individuals trying to deter a predator, and they usually attract conspecifics as well as some heterospecific receivers to the caller position (Flasskamp, 1994; Pavey & Smyth, 1998; Pettifor, 1990). Both the intensity of mobbing and its success in deterring the predator are positively related to the size of the group gathered by the caller (Picman, Leonard & Horn, 1988; Robinson, 1985; Verbeek, 1985). Thus, contrarily to flee alarm calls, the functional support of mobbing calls requires the sender to be easily localizable (Marler, 1957; Yorzinski & Patricelli, 2009; Hurd, 1996), a sound property that could be enhanced by both broadband frequencies and short duration. In his seminal work on the distinctiveness of alarm calls function according to these specific acoustic features, Marler (1955) suggested that these functional supports should lead to convergence of the related acoustic signals in diverse taxa. Thus, mobbing calls provide us a clear functional support to anchor comparative analyses on the evolution of acoustic communication. Nevertheless, to our knowledge, such a comparative analysis is still lacking. Indeed, few studies investigated acoustic variations of mobbing calls across bird species (Latimer, 1977; Ficken & Popp, 1996, Proppe *et al*., 2010; Wheatcroft & Price, 2014; Billings, 2018), but none quantitatively compared these variations to those observed on vocalizations observed in other functional supports (but see Latimer, 1977; Wheatcroft & Price, 2014). Moreover, among the very few studies that compared the divergence of acoustic signals according to their respective functional support (Hu & Cardoso, 2010; Martin *et al*., 2011, Potvin *et al*., 2011; Sturge *et al*., 2016 on calls and songs), all did not considered within species variations or performed separate phylogenetic analyses for each acoustic signal. This is somewhat problematic since ignoring within species variance can lead to biased and imprecise estimates (Ives *et al*., 2007) and because closely species tend to exhibit more similar patterns than expected by chance (Freckleton *et al*., 2002).

In this study, we investigated across 23 songbird species the relative divergence of acoustic features between two types of vocalization, respectively mobbing calls and territorial songs. On a structural level, songs are usually longer and more complex, involving a variety of differences notes and syllables; mobbing calls are often short with simple frequency pattering (Marler & Slabbekoorn, 2004) although recent studies found complex mechanism enabling information transfer (Engesser *et al*., 2016; Suzuki *et al*., 2016). The two main aims of this study are to ask whether divergence varies according to (1) the functional support (i.e. mobbing calls versus territorial songs) controlling for phylogenetic inertia and (2) the environmental contrast, namely closed versus semi-open habitat.

MATERIALS AND METHODS

Species selection

To be included in our study, species had to meet the following two requirements: (1) knowledges of the vocal repertoire were sufficient and (2) available good quality records. We further restricted our studies on nine oscines families in order to minimize morphological differences (body size: mean ± se = 14 ± 0.71 cm, range 10-28; body weight: mean ± se =

17.91 ± 2.81g, range 9-75): 1 species from the Fringillidae, 1 species from the Meliphagidae, 2 species from the Muscicapidae, 8 species from the Paridae, 3 species from the Parulidae, 3 species from the Sittidae, 1 species from the Thraupidae, 2 species from the Troglodytidae, 2 species from the Vireonidae. A total of 23 species have been chosen. Openness of the habitat used by each species was inferred from Handbooks of birds and oiseaux.net website (http://www.oiseaux.net/). According to this classification, 11 species are forest birds, 11 live in semi-open habitat and one occurs in open habitat (i.e. the white-collared seedeater *Sporophila torqueola*). For further analyses semi-open and open categories were regrouped (hereafter semi-open habitat).

Acoustic recordings and analysis

We broadcast a series of Pygmy Owl calls *Glaucidium passerinum* and mobbing calls during which we recorded mobbing calls of European species (25 total individuals among 7 species) with a Fostex FR2LE digital recorder connected to a Sennheiser ME67-K6P microphone (see Dutour *et al*., 2016). Robert Magrath and David Wheatcroft courtesy gave us records of the noisy miner (*Manorina melanocephala*) (*n* = 10) and Eurasian wren (*Troglodytes troglodytes*) (*n* = 1) mobbing calls in similar condition. We completed our data set using the Macaulay Library (Cornell Lab of Ornithology, http://macaulaylibrary.org) and the Xeno Canto online database (www.xeno-canto.org). We did not use recordings of juveniles, which might be still learning vocalization. We obtained measurements of acoustic features by measuring spectrograms in Avisoft Saslab, following established method (Dutour *et al*., 2017). We selected up to 10 mobbing calls recordings per species (on average 4.52 ± 1.72 SD; range 2-10) and 5 territorial songs recordings per species (on average 4.87 ± 0.46 SD; range 3-5). A total of 216 individual records were measured. Before for each individual, we measured on average 7.4 signals ± 0.23 SD (range 1-10) and selected the middle signal (216 acoustic signals from 216 individuals were used). For each sound recording, we measured 7 acoustic features: spectral features (1) peak frequency (the frequency for which amplitude is maximum in Hz); (2) maximum frequency (highest frequency of the call in Hz); (3) minimum frequency (lowest frequency of the call in Hz); (4) frequency bandwidth (differences in Hz between maximum frequency and minimum frequency measure on a linear amplitude spectrum (threshold -20dB)); and three acoustic features involved in temporality and complexity : (5) duration (s); (6) number of elements; (7) number of different elements per vocalization. An element was defined as a single note clearly separated from other elements by a visible temporal pause. From these features, we calculated the mean note duration (signal duration /

number of elements) and note variability (= number of different elements / number of elements).

Phylogenetic framework

We based our analyses on the phylogenetic tree distributions from the BirdTree database (Jetz et al. 2012; http://birdtree.org). For both ‘Hackett’ and ‘Ericson’ backbones, we sampled 100 trees (with 9993 or 6670 Operational Taxonomic Units, OTUs each) which were pruned to generate tree distributions for all species except the Japanese tit (not available in the database) in our dataset. Based on these distributions, we used TreeAnnotator version 2.4.7 to generate four maximum clade credibility (MCC) trees (i.e. one tree for each method), setting branch lengths equal to ‘Common Ancestor’ node heights. The four final composite trees differed slightly in topology, and finally we used the composite tree based on the Ericson 9993 method. Because the Japanese tit was the nearest species to the great tit and they was hybridization between them (Paeckert *et al*., 2005; Kvist & Rytkönen, 2006; Johansson *et al*., 2013), we added an arbitrary value for this species to obtain the final tree. The phylogenetic variance-covariance matrix was obtained from the transformation of the final phylogenetic tree under Brownian motion model.

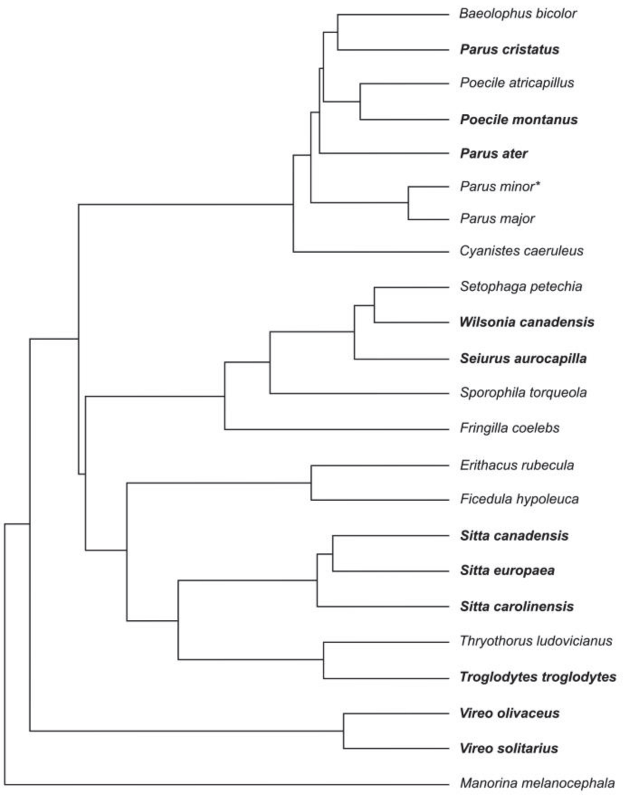

Figure 1. Phylogenetic tree showing 23 species used for analysis of territorial songs and mobbing calls. 11 species in bold are species inhabiting forests and 12 others inhabiting semi-open habitats. *we added an arbitrary value in the tree for *Parus minor* because it was not included in the phylogenetic tree of Jetz *et al*., 2012 and Jetz *et al*., 2014.

Statistical analyses

We first carried out a linear discriminant analysis (LDA) on the whole dataset (216 records collected on 23 species) to identify synthetic component of the acoustic variables that best segregate the two types of vocalization, i.e. mobbing calls and territorial songs. The maximum frequency was found strongly correlated with frequency bandwidth (r= 0.86, p < 0.001). This acoustic feature was thus discarded for further analyses and LDA was thus restricted to duration, mean note duration (= signal duration / number of elements), note variability (= number of different elements / number of elements), peak frequency, minimum frequency and frequency bandwidth. The first three linear discriminants explained a total of 74.63% of variance. (LD1: 31.31%, LD2: 26.37% and LD3: 16.95%). Aspects of call complexity and temporality contributed to LD1 (mean note duration: factor loading -0.53 and note variability: factor loading 0.73) and LD3 (duration -0.38). Spectral features of acoustic signals load onto LD2 (frequency bandwidth: factor loading 0.85) and LD3 (minimum frequency: factor loading 0.65 and peak frequency: factor loading 0.53). Then, we obtained coordinates of 216 acoustic signals on the first three linear discriminants

We constructed phylogenetic generalized linear mixed models using GIMMIX procedure (SAS Institute Inc. 2012) to estimate the relative divergence of acoustic features according to the type of vocalization while controlling for the effect of habitat closure. We first constructed a multivariate model specifying both the three first LDA components (LD1, LD2 and LD3) as dependent variables using a normal distribution for the error term, and both the type of vocalization, the habitat and their interactive effects as the fixed explanatory terms. For this purpose, we followed the methodology proposed by De Lisle (2018) to specify the effect of the phylogenetic covariance matrix as random phylogenetic variance components for the three dependent variables as well as the corresponding residual variance-covariance parameters. We also allowed variance heterogeneity on residual variance-covariance parameters according to the type of vocalization. However, it was not possible to estimate separately within- and between- species (residual) variance in this multivariate phylogenetic model framework. Restricted maximum pseudo-likelihood optimization method was used to fit the model since other methods are not feasible when introducing covariance parameter in the residual matrix of generalized linear mixed models. We first examined the significance of the phylogenetic variance components using a Likelihood Ratio Test on the full model. As likelihood ratio test can be biased when performed on maximum pseudo-likelihood estimates, we therefore used maximum likelihood optimization method (SAS Institute Inc. 2012) when possible (i.e. when the error term follows a Normal distribution as here) to perform the test. If non-significant, the phylogenetic effect was then discarded for further analyses. The significance of fixed effects was then examined using a non-sequential F test and the Kenward-Roger method to approximate the residual df. All non-significant fixed terms were then successively removed to obtain the final model.

As LD components represent a linear combination of acoustic features, which can be problematic for the interpretation of the effects on acoustic features, and because our multivariate phylogenetic generalized mixed model does not allow to properly estimate within-between species variance components, we also performed univariate phylogenetic generalized mixed model for each LD component as well as for each acoustic features involved in LD components (total duration, mean note duration, note variability, minimal frequency, peak frequency and frequency bandwidth). Vocalization duration and mean note duration were Log transformed prior the analysis and spectral variables (minimal frequency, peak frequency and frequency bandwidth) were standardized using square root transformation. All variables except the note variability were introduced using a Normal residual term error. The note variability was modeled using a logit link and a beta distribution for the error term in order to accommodate overdispersion. Moreover, the within between species variance components were introduced in the R side of the model using a compound symmetry covariance matrix and allowing heterogeneity according to the type of vocalization. The method used to fit the model, test the significance of variance components and the one of fixed explanatory terms were the same as above. Moreover, for each dependent variable, we also computed the species intraclass correlation coefficient (ICC) for both type of vocalization as the proportion of the between species variance relative to the total variance (i.e. $ICC = \frac{\sigma^2_{between\,spc.}}{\sigma^2_{between\,spc.} + \sigma^2_{within\,spc.}}$). In the case of the note variability the ICC was computed using adjustment for the logit scale (i.e. $= \frac{\sigma^2_{between\,spc.}}{\sigma^2_{between\,spc.} + \sigma^2_{within\,spc.} + \pi^2/3}$).

RESULTS

Multivariate phylogenetic analyses on Linear Discriminant

According to the multivariate phylogenetic model, a reduced but statistically significant part of the phenotypic variance expressed through the three main discriminant components was explained by the phylogenetic non independency among species ($P < 0.0001$ see Table 1 Supplementary Material), with a substantially higher contribution for LD1 than for LD2 and LD3, and a very low phylogenetic covariance between discriminant components (see Table 1

Supplementary Material). Overall, the difference between the three LD components observed according to the type of vocalization also varied according to the habitat as revealed by the significance of the three way interaction ($F_{1,103.9} = 8.23$; $P = 0.0005$). Univariate analyses performed separately for each LD component revealed that phylogenetic inertia is significant for LD1 and LD3 but not for LD2 (see Table 2 Supplementary Material). Moreover, these analyses also indicate a significant higher variance heterogeneity among mobbing calls than among territorial songs, both concerning the between species variance and the residual variance (i.e. the within species variance), and whatever the LD component (see Table 2 Supplementary Material).

Phylogenetic analyses on the complexity and temporal features of acoustic signals

The phylogenetic inertia was found non-significant on the duration and a large ICC was estimated for both types of vocalization although slightly higher in the case of territorial songs than in the case of mobbing calls (respectively 0.81 and 0.90 for mobbing calls and territorial songs, see Table 1). There was also a higher variance heterogeneity among mobbing calls than among territorial songs, both concerning the between species variance and the residual variance. The duration only varies according to the type of vocalization and was found significantly higher for territorial songs than for mobbing calls (Vocalization type: $F_{1,33.2} = 8.97$; $P = 0.005$; Habitat status: $F_{1,33.1} = 0.83$; $P = 0.369$; interaction term: $F_{1,31.9} = 0.11$; $P = 0.748$; Fig. 2a). We detected a significant phylogenetic inertia on mean note duration (Table 1). As for duration, there was a higher variance heterogeneity among mobbing calls than among territorial songs, both concerning the between species variance and the residual variance. Nevertheless, contrarily to duration, ICC was found slightly higher in the case of mobbing calls than in the case of territorial songs (respectively 0.75 and 0.65 for mobbing calls and territorial songs, see Table 1). Moreover, neither the type of vocalization nor the habitat significantly affected the mean note duration of the vocalization (Vocalization type: $F_{1,38.9} = 0.27$; $P = 0.607$; Habitat status: $F_{1,39.1} = 0.09$; $P = 0.768$; interaction term: $F_{1,37.7} = 0.00$; $P = 0.992$; Fig. 2b). We did not detect a significant phylogenetic inertia on the note variability (see Table 1), and the within species variance was also higher among mobbing calls than territorial songs. However, ICC was low whatever the type of vocalization (i.e. 0.13 for each type of vocalization). Moreover, the note variability does not significantly vary according to the type of vocalization nor according to the habitat (Vocalization type: $F_{1,42.8} =$

0.01; P = 0.920; Habitat status: $F_{1,41.3} = 0.53$; P = 0.469; interaction term: $F_{1,41.3} = 1.46$; P = 0.234; Fig. 2c).

Phylogenetic analyses on the spectral features of acoustic signals

We found a significant phylogenetic inertia concerning the peak frequency (Table 1). Moreover, while the ICC was relatively low in the case of mobbing calls (0.4 see Table 1), it was null in the case of territorial songs (see Table 1), although the residual variance was substantially higher among mobbing calls than among territorial songs. Furthermore, the difference of peak frequency according to the type of vocalization significantly varied according to the habitat as revealed by the significance of the two way interaction (Vocalization type: $F_{1,150.2} = 14.45$; $P < 0.001$; Habitat status: $F_{1,9.2} = 0.04$; P = 0.842; interaction term: $F_{1,157.3} = 18.20$; P < 0.001; Fig. 2d): as indicated by the sliced tests, while the peak frequency was significantly higher for mobbing calls than for territorial songs among semi-open species ($F_{1,171} = 38.3, P < 0.0001$), no difference was found according to the type of vocalization among forest species ($F_{1,142.6} = 0.09, P = 0.76$). A significant phylogenetic inertia was also detected on the minimal frequency (Table 1). The ICC also greatly varied according to the type of vocalization, since it is relatively large in the case of mobbing calls (0.71, see Table 1) but relatively low in the case of territorial songs (0.11, see Table 1). Furthermore, both the between species variance and the residual variance were higher among mobbing calls than among territorial songs. The minimal frequency did not significantly vary according to the habitat but it was found significantly higher in the case of territorial songs than in the case of mobbing calls (Vocalization type: $F_{1,22.2} = 11.16$; P = 0.003; Habitat status: $F_{1,19.7} = 0.75$; P = 0.398; interaction term: $F_{1,21.2} = 0.03$; P = 0.863; Fig. 2e). We did not detect a significant phylogenetic inertia on the frequency bandwidth. Contrarily to the other two spectral acoustic features, the ICC was similarly large whatever the type of vocalization (respectively 0.66 and 0.74 for mobbing calls and territorial songs, see Table 1) and the between variance was significantly lower among mobbing calls than among territorial songs (while the residual variance did not differ according to the vocalization type). Moreover, the frequency bandwidth was significantly higher for mobbing calls than territorial songs but not affected by habitat (Vocalization type: $F_{1,42.5} = 19.54$; P <0.001; Habitat status: $F_{1,42.92} = 0.45$; P = 0.842; interaction term: $F_{1,41.4} = 0.35$; P = 0.557; Fig. 2f).

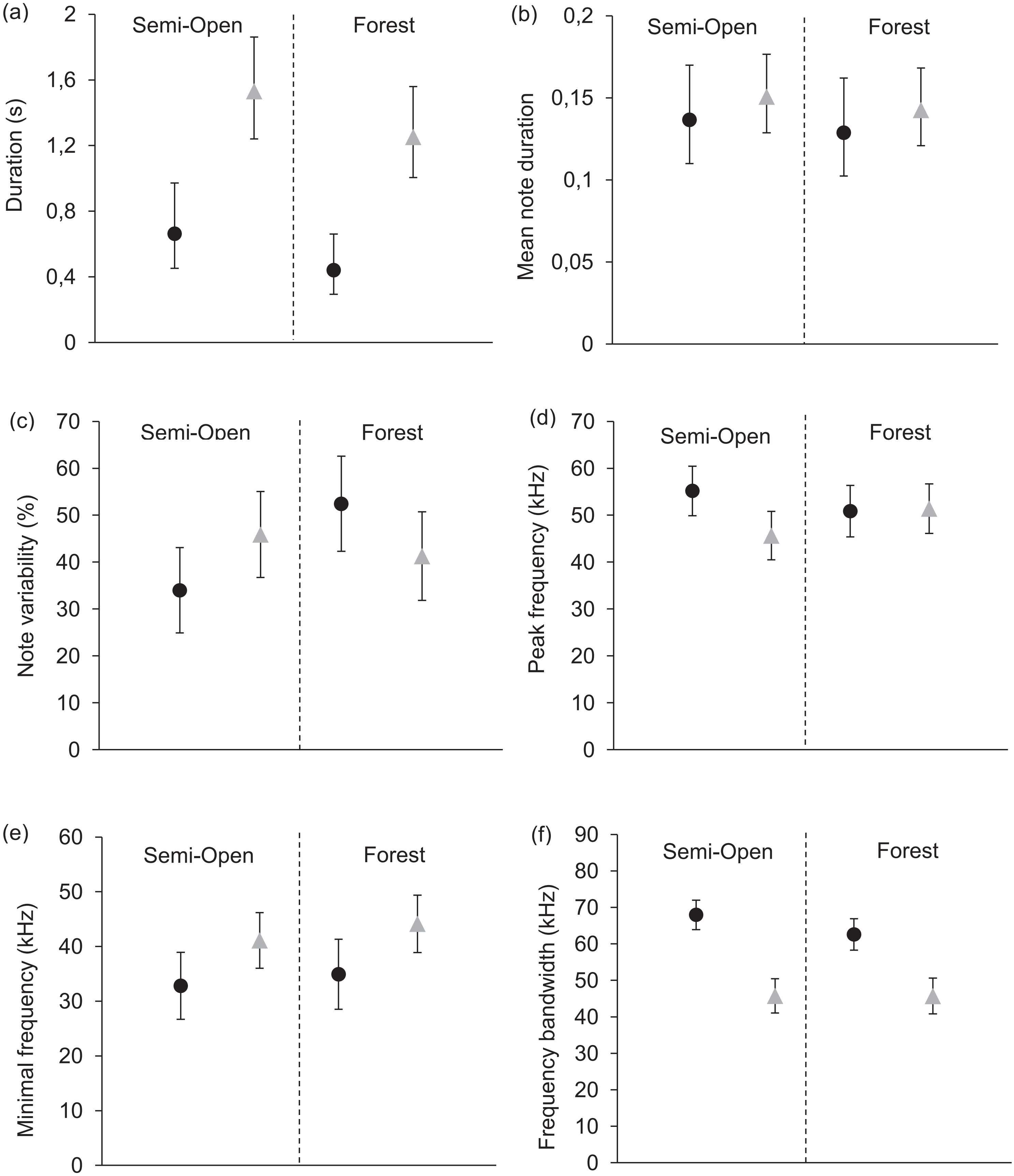

Figure 2. Variation of acoustic features according to the type of vocalization (territorial songs grey triangle or mobbing calls black circle) and habitat status (semi-open or closed) (mean estimate ± se of the fixed effects). (a) duration, (b) mean note duration (= signal duration / number of elements), (c) note variability (= number of different elements / number of elements), (d) peak frequency, (e) minimum frequency and (f) frequency bandwidth

Table 1. Phylogenetic analyses on six features of acoustic signals. σ^2_{phy} for the random phylogenetic variance component; σ^2_b and σ^2_w respectively for the between species variance and the within species variance; M and T subscripts respectively for mobbing calls and territorial songs. P values are computed from likelihood ratio tests (LRT) for the random effects, and from F tests for the fixed effects. † LRT of residual variance heterogeneity according to the type of vocalization. ǂ LRT of a different between species variance according to the type of vocalization. For note variability: ǂ* reduced model did not converge, preventing the computation of the LRT. For peak frequency: (ne)*: not estimable (i.e. estimated at the lower bound). For frequency bandwidth: **: σ^2_{phy} estimated below the lower bound (<0).

Acoustic feature	Random effects	Estimate (SE)	LRT	*P*
Duration	σ^2_{phy}	0.006 (0.006)	$\chi^2_1 = 1.2$	0.273
	σ^2_{bM}	1.676 (0.554)	$\chi^2_1 = 125^{ǂ}$	<0.001
	σ^2_{bT}	0.519 (0.164)		
	σ^2_{wM}	0.383 (0.0603)	$\chi^2_1 = 67.8^{\dagger}$	<0.001
	σ^2_{wT}	0.058 (0.009)		
Mean note duration	σ^2_{phy}	0.005 (0.003)	$\chi^2_1 = 4.4$	0.0359
	σ^2_{bM}	0.406 (0.159)	$\chi^2_1 = 81.2^{ǂ}$	<0.001
	σ^2_{bT}	0.118 (0.090)		
	σ^2_{wM}	0.136 (0.021)	$\chi^2_1 = 12.3^{\dagger}$	0.0004
	σ^2_{wT}	0.063 (0.009)		
Note variability	σ^2_{phy}	0.018 (0.018)	$\chi^2_1 = 2.2$	0.138
	σ^2_{bM}	0.544 (0.182)	Not estimable ǂ*	
	σ^2_{bT}	0.516 (0.163)		
	σ^2_{wM}	0.156 (0.024)	$\chi^2_1 = 11.1^{\dagger}$	0.0009
	σ^2_{wT}	0.060 (0.009)		

	scale*	0.3061		
Peak frequency	σ^2_{phy}	1.90 (0.68)	$\chi^2_1 = 17.84$	<0.0001
	σ^2_{bM}	54.57 (25.49)	$\chi^2_1 = 15.80^{‡}$	0.0004
	σ^2_{bT}	0 (ne)*		
	σ^2_{wM}	82.02 (12.87)	$\chi^2_1 = 17.2^{†}$	<0.0001
	σ^2_{wT}	33.36 (4.95)		
Minimal frequency	σ^2_{phy}	2.02 (1.18)	$\chi^2_1 = 10.4$	0.0012
	σ^2_{bM}	140.13 (52.40)	$\chi^2_1 = 65.9^{‡}$	<0.0001
	σ^2_{bT}	3.72 (22.02)		
	σ^2_{wM}	56.24 (8.82)	$\chi^2_1 = 9.3^{†}$	0.0023
	σ^2_{wT}	28.87 (4.33)		
Frequency bandwidth	σ^2_{phy}	-0.14 (1.62)**	$\chi^2_1 = 0$	1
	σ^2_{bM}	176.20 (60.31)	$\chi^2_1 = 117.2$	<0.0001
	σ^2_{bT}	245.40 (81.92)		
	σ^2_{wM}	85.92 (13.45)	$\chi^2_1 = 0.1$	0.7518
	σ^2_{wT}	91.08 (13.67)		

DISCUSSION

In the present study, by analysing signals emitted by 23 bird species, we show that divergence (or convergence) of acoustic features varies according to their functional support (mobbing calls versus territorial songs) and the environmental contrast.

Effect of phylogeny

Overall, we did not detect a strong phylogenetic signal whatever the acoustic feature: it was only significant for three acoustic features (mean note duration, peak frequency and minimal frequency) and was relatively weak according to its variance component estimate. Most of the comparative studies on bird vocalization also reported a relatively weak but varying phylogenetic signal according to the acoustic features (Tobias *et al*., 2013; Billings, 2018). However, using a larger dataset than previously done, Pearse *et al*. (2018) reported a large variation of the phylogenetic signal (from very weak to moderate) according to the acoustic features. Since our dataset was restricted to nine oscine families, the relative effect of shared ancestry concerning characters involved in sound production or modulation such as syrinx morphology (Ryan & Brenowitz, 1995) or beak shape (Derryberry *et al*., 2018) is likely reduced. Moreover, most of the studies also reported an important effect of the body size on several acoustic features (Wallschäger, 1980; Ryan & Brenowitz, 1985; Derryberry *et al*., 2018; Billings, 2018). But our studies was not designed to track such an effect since we selected species to minimize size difference among them, and indeed, none of the acoustic features were found to vary according to body size (results not shown). Thus, one should not be surprised to find a weak phylogenetic signal in our studies.

Different acoustics features according to the vocalization types

The two vocalization types studied are used for different purpose. Mobbing calls are emitted against predator (Yorzinski & Patricelli, 2009) while territorial songs play an important role in sexual and social communication (Catchpole & Slater, 2003). As predicted, the duration was found significantly higher for territorial songs than for mobbing calls. This pattern was consistent with previous studies (Marler, 1955; Marler & Slabbekoorn, 2004). When we focused on spectral features, we found that for the peak frequency, the difference according to the type of vocalization varied according to the habitat (see paragraph below). Moreover, the minimal frequency was significantly higher for territorial songs than for mobbing calls. Hand in hand with the frequency bandwidth which was higher for mobbing calls than territorial songs making thus the sender easier to localize when mobbing than when singing as expected (Marler, 1955; Dooling & Searcy, 1985; Aubin & Jouventin, 2002). This is particularly important since both the intensity of mobbing and its success in deterring the predator are positively related to the size of the group gathered by the caller. On a structural level, songs are usually thought to be more complex than mobbing calls, involving more distinct notes than mobbing calls (Marler & Slabbekoorn 2004). We also found that songs involve a larger number of distinct elements (mean ± se: number of elements: territorial songs = 14 ± 1.1; mobbing calls: 6.2 ± 0.5; number of different elements: territorial songs = 4.99 ± 0.5; mobbing calls: 1.3 ± 0.1). Note, however, that we did not found difference of structural complexity between the two types of vocalization when we corrected the number of distinct elements (note variability) by the number of elements. We also found a similar pace between mobbing calls and songs as revealed by the mean note duration. Thus, when controlling for the difference of duration between the two types of vocalization, songs do not appear more complex than mobbing calls. Complexity in mobbing calls has been documented by Ficken and Popp since 1996 and more and more studies demonstrate an unsuspected level of complexity and sophistication in mobbing calls. Indeed, recent studies found complex mechanism enabling information transfer (Engesser *et al*., 2016; Suzuki *et al*., 2016; Suzuki *et al*., 2017). Data collected on note variability are likely to be overdispersed. This result is probably due to the fact that we have missed important individuals during our acoustical sampling although the number of individuals selected was in the most common range (e.g. Morinay *et al*., 2013; Wheatcroft & Price, 2014; Derryberry *et al*., 2018). More individuals are needed to explore the divergence of this complexity feature according to functional support.

Effect of habitat

Using the physics of sound energy propagation as criteria, several authors found that species living in densely vegetated habitats generally have lower peak frequencies and more narrow frequency bandwidth than species inhabiting more open areas (Chapuis, 1971; Morton, 1975; Vélez *et al*., 2015). In addition, birds with more complex songs tend to be found within more complex landscapes (Pearse *et al*., 2018). In our studies, the significant three-way interaction indicates that LD components differences according to the type of vocalization also vary according to the habitat. Nevertheless separate analyses on each LD components did not reveal significant differences between vocalization types according to the habitat (see supplementary material 2). Such a discrepancy could be due to the flaws of our LD components since most of the acoustic features substantially loaded on more than one LD component, and the variance explained by each LD component was relatively moderate (<33%). Analyses performed for each acoustic feature indicate that one of them, the peak frequency, is higher for mobbing calls than territorial songs among species living in semi-open habitat, but not among forest species. The pattern found for semi-open habitat may be related to the transmission features of each type of vocalization. High frequencies are more attenuated than low frequency during propagation (Mathevon *et al*., 1997, Lengagne *et al*., 1999b) while it is usually suggested that territorial calls are intended to a more distant audience than calls which are intended to a nearby audience (Martin *et al*., 2011). The absence of difference between the two types of vocalization and between the two types of habitat may be due to phenotypic plasticity. Indeed, it is know that species adjust their vocalizations to match their territory's transmission properties (Hunter & Krebs, 1979; Slabbekoorn & Peet, 2003). An additional analysis taking account the exact location where individuals were recordings is required. Finally, the lack of relationship between the other spectral features and habitat may be due to the fact that we had not enough contrast among habitats. Indeed, among the 23 studied species, just one of them lived in open field (this species was regrouped with species inhabiting semi-open for statistical reasons). This could be due to a bias of recording sampling performed in open field and found in sound data base. More probably, we suggested that in these open habitats few bird species used mobbing behavior. According to Billings (2018), 20% of species exhibiting mobbing behavior are living in open habitats.

Relative divergence of acoustic feature according to the type of vocalization

We found a substantial within species variance for the two types of vocalization, illustrating the importance of considering residual variance in analyses. This result indicate that not only species-specific mean values of acoustic trait, but also its variance within species can shape the rate of divergence of species (Garamszegi & Møller, 2017). This variation could emerge due to phenotypic plasticity or true between-individual differences. However, in the present study, it is not possible to segregate between individuals variations from intra-individual variations since birds were not repeatedly recorded. Our results revealed that within and between species variances for each type of vocalization vary according to the acoustic feature, suggesting that the divergence rate of acoustic features across species depends on the type of vocalization. The interpretation of variance partitioning could be flawed for two acoustic features that we therefore no further discuss: the note variability given the nature and the statistical overdispersion of the metric used (i.e. a proportion), and peak frequency given the interactive effect of habitat and the type of vocalization (see previous section). For duration, our results indicate that territorial songs diverge between species compared to mobbing calls which present high variance heterogeneity, indicating that selection pressures for these acoustic features seem to be less pronounced for mobbing calls. In particular, songs are more stereotypical than mobbing calls. Indeed, duration of mobbing calls could be strongly context dependent as suggested by the influence of the physiological state (i.e. arousal) of the caller or the risk posed by the predator (Templeton et al., 2005). For mean note duration, our results indicate that mobbing calls which present high variance heterogeneity are nevertheless more divergent across species than territorial songs. An hypothesis, dealing with acoustic communication system complexity, may explain this divergence. Calls are structurally complex for some species such as tits and chickadees because of the presence of different elements encoding different information contrary to other species. Species with complex calling system may encode much information within a limited time because situation is risky. The divergence between species can also reflect the mobbing propensity: low mean note duration in a species may be related to a low propensity to harass. For minimal frequency, our results indicate that territorial songs among species are much less divergent than mobbing calls. This is intriguing since one should expect a directional selection pressure imposing on birds to produce minimal frequency in their mobbing calls but not in the songs. Selection on species' trait such as body size (Derryberry *et al*., 2018) has been found to severely constrain minimal frequency in bird songs. Thus, it could be that higher variations of minimal frequency of mobbing calls across species result from variations of bioacoustics constraints prevailing among species. Finally, for frequency bandwidth the between variance was significantly lower among mobbing calls than among territorial songs and the residual variance did not differ according to the vocalization type, indicating that mobbing calls are much more similar across species than territorial songs for this feature. This result suggests that convergent evolution on mobbing calls may outweigh the contribution of divergent evolution.

Mobbing calls have a broader frequency bandwidth than territorial songs and this characteristic is shared with aggressive and distress signals in birds (Marler, 1957; Wheatcroft & Price, 2014) and mammals (August & Anderson, 1987). The convergent evolution on frequency bandwidth in mobbing calls could be explained by relationship between the physical structures of sounds and the motivation underlying their use (Morton, 1977). Sounds with wide bandwidth and low-frequency are consistently associated with hostile and aggressive motivations and could be evolved by convergence (Morton, 1977; August & Anderson, 1987). The second mechanism by which convergent selection acts on mobbing calls should be that individuals with convergent signals are more successful in deterring predator. According to this hypothesis, Russ *et al.* (2004) also proposed that selection may favour convergence in the structure of distress calls among bat species, if attracting heterospecifics increases the chance of repelling predators by mobbing. Mobbing calls communicate the presence of a predator to heterospecific as well as conspecifics and it is possible that individual produce mobbing calls displays that resemble mobbing calls of sympatric species exploiting the sensory predisposition of heterospecifics leading to convergence of signals features. Nevertheless, we showed that such rules seem not to be the sole explanation. Indeed, blue tit (*Cyanistes caeruleus*) respond to allopatric mobbing calls but its response to black-capped chickadee (*Parus atricapillus*) is low although mobbing calls of these two species are much closed (Dutour *et al*., 2017). The large frequency band shared among species indicates that this spectral feature is essential during mobbing. As for mobbing, it appears that wide spectrum signals recur in the vocalisations of many colonial birds (White & White, 1970; Mathevon, 1997; Charrier *et al*., 2001), i.e. in an environment where the estimation of the direction of a signal is particularly useful. It would be interesting to extend the comparison of evolutionary rate according to the type of vocalization to the flee alarm calls. Indeed, as noted by Klump (2000), the acoustic features of these calls should make the sender difficult to localize so that convergence of flee alarm calls in the opposite direction of mobbing calls could be expected (Marler, 1955; Marler, 1957).

Conclusions

To conclude, our results suggest that the functional support and habitat may cause signals divergent or convergent evolution in birds. Research into the signal evolution has mostly focused on one functional support and more studies taking into account several functional supports would be of substantial value. To increase their localization and increase the chance of repelling predators, birds should arrive promptly at the place where the predator has been found to mob. Such localization process probably explains why all birds' species converge towards a similar acoustic solution to be localized and exhibit in their mobbing call a large frequency band. The same results might be found on mammal species that use mobbing calls to harass predators.

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SUPPLEMENTARY MATERIAL

APPENDIX 1. Multivariate phylogenetic analyses on Linear Discriminant

Table 1. Results of the multivariate phylogenetic model. σ^2_{phy} , σ^2_{phycov} respectively for random phylogenetic variance and covariance estimates; σ^2_{res} for residuals; each discriminant component is indicated by the corresponding subscript (i.e. LD1, LD2 and LD3); M for mobbing calls and T for territorial songs. P values are from Likelihood ratio tests for the random effects, and from F tests for the fixed effects.

Random effects	**Estimate (SE)**	**LRT**	***P***
$\sigma^2_{phy\ ld1}$	0.160 (0.051)	$\chi^2_6 = 358.57$	<0.0001
$\sigma^2_{phy\ ld2}$	0.102 (0.034)		
$\sigma^2_{phycov\ ld1\ ld2}$	0.033 (0.012)		
$\sigma^2_{phycov\ ld1\ ld3}$	-0.012 (0.014)		
$\sigma^2_{phycov\ ld2\ ld3}$	0.003 (0.008)		
$\sigma^2_{ld1\ M}$	-0.004 (0.006)		
$\sigma^2_{ld2\ M}$	2.505 (0.193)	$\chi^2_6 = 120.7$	<0.0001
$\sigma^2_{ld3\ M}$	2.430 (0.197)		
$\sigma^2_{phy\ ld1}$	2.139 (0.185)		
$cov_{\ ld1\ ld2\ M}$	-0.305 (0.271)		
$cov_{\ ld1\ ld3\ M}$	-0.654 (0.270)		
$cov_{\ ld2\ ld3\ M}$	-1.094 (0.260)		
$\sigma^2_{ld1\ T}$	0.850 (0.072)		
$\sigma^2_{ld2\ T}$	0.937 (0.082)		
$\sigma^2_{ld3\ T}$	0.946 (0.083)		
$cov_{\ ld1\ ld2\ T}$	0.049 (0.114)		
$cov_{\ ld1\ ld3\ T}$	0.254 (0.118)		
$cov_{\ ld2\ ld3\ T}$	0.067 (0.117)		
Fixed effects		F test	
LD component		$F_{2,31} = 0.43$	0.6564
Habitat status		$F_{1,18.1} = 1.15$	0.2972
LD component*Habitat status		$F_{2,29} = 1.12$	0.3396
Vocalization type		$F_{1,139.4} = 43.72$	<0.0001
LD component* Vocalization type		$F_{2,104} = 13.99$	<0.0001
Vocalization type*Habitat status		$F_{1,139.3} = 6.98$	0.0092
LD component*Vocalization type* Habitat status		$F_{1,103.9} = 8.23$	0.0005

APPENDIX 2. Univariate phylogenetic analyses on Linear Discriminant

Univariate analyses performed separately for each LD component revealed that phylogenetic inertia is significant for LD1 and LD3 but not for LD2 (Table 2). Moreover, these analyses also indicate a significant higher variance heterogeneity among mobbing calls than among territorial songs, both concerning the between species variance and the residual variance (i.e. the within species variance), and whatever the LD component. Concerning LD1, the Intraclass Correlation Coefficient (ICC) was rather large whatever the type of vocalization although slightly lower for mobbing calls (respectively 0.70 and 0.79 for mobbing calls and territorial songs, see Table 1). However, neither the type of vocalization nor the habitat significantly affected LD1 (Vocalization type: $F_{1,26.1} = 0.14$; $P = 0.7149$; Habitat status: $F_{1,29.6} = 0.51$; $P = 0.4810$; interaction term: $F_{1,25.2} = 0.57$; $P = 0.4562$). Concerning LD2, the ICC was also substantially lower in the case of mobbing calls than in the case of territorial songs (respectively 0.63 and 0.78, see Table 2). Contrarily to the first discriminant components, LD2 significantly differed between both types of vocalization although it did not significantly vary according to the habitat (Vocalization type: $F_{1,42.8} = 9.82$; $P = 0.0031$; Habitat status: $F_{1,42.8} = 1.75$; $P = 0.1925$; interaction term: $F_{1,42} = 2.47$; $P = 0.1232$). In particular, LD2 was significantly higher in the case of mobbing calls than territorial songs. Contrarily to the other two discriminant components, we found a substantially higher ICC for mobbing calls than territorial songs in the case of LD3 (respectively 0.76 and 0.53, see Table 2). However, similarly to LD1, LD3 neither varied between both types of vocalization nor according to the habitat (Vocalization type: $F_{1,26} = 0.87$; $P = 0.3583$; Habitat status: $F_{1,22.3} = 0.03$; $P = 0.8596$; interaction term: $F_{1,24.7} = 0.67$; $P = 0.4219$).

Table 2. Phylogenetic analyses for LD1, LD2 and LD3. σ^2_{phy} for the random phylogenetic variance component; σ^2_b and σ^2_w respectively for the between species variance and the within species variance; M and T subscripts respectively for mobbing calls and territorial songs. P values are computed from likelihood ratio tests (LRT) for the random effects, and from F tests for the fixed effects. † LRT of residual variance heterogeneity according to the type of vocalization. ǂ LRT of a different between species variance according to the type of vocalization.

Linear Discriminant	**Random effects**	**Estimate (SE)**	**LRT**	***P***
LD1	σ^2_{phy}	0.080 (0.042)	$\chi^2_1 = 10.1$	0.0014
	σ^2_{bM}	3.707 (1.707)	$\chi^2_1 = 91.5^{ǂ}$	<0.0001
	σ^2_{bT}	2.418 (1.399)		
	σ^2_{wM}	1.581 (0.249)	$\chi^2_1 = 16.9^{\dagger}$	<0.001
	σ^2_{wT}	0.6416 (0.096)		
LD2	σ^2_{phy}	0.025 (0.025)	$\chi^2_1 = 1.4$	0.236
	σ^2_{bM}	2.996 (1.347)	$\chi^2_1 = 87.42^{ǂ}$	<0.0001
	σ^2_{bT}	2.675 (1.277)		
	σ^2_{wM}	1.747 (0.274)	$\chi^2_1 = 15.2^{\dagger}$	<0.0001
	σ^2_{wT}	0.744 (0.112)		
LD3	σ^2_{phy}	0.021 (0.015)	$\chi^2_1 = 5.1$	0.0239
	σ^2_{bM}	4.176 (1.958)	$\chi^2_1 = 106.3^{ǂ}$	<0.0001
	σ^2_{bT}	0.886 (0.870)		
	σ^2_{wM}	1.320 (0.207)	$\chi^2_1 = 5.4^{\dagger}$	0.0201
	σ^2_{wT}	0.796 (0.119)		

Article 6 : Effect of compositional syntax manipulation on heterospecific response to mobbing call

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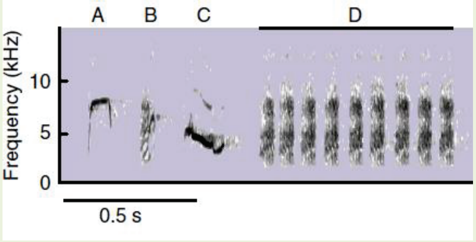
Behavioral Ecology and Sociobiology, soumis août 2018

Problématique :

Une étude récente a mis en évidence l'utilisation de la syntaxe compositionnelle (i.e. mots qui forment une phrase) chez la mésange de Chine, *Parus minor* (Encadré 1). Ce mécanisme est-il généralisable à d'autres espèces ? Dans la mesure où le harcèlement implique de la communication entre espèces, la syntaxe compositionnelle a-t-elle pu évoluer à échelle interspécifique ?



Un cri de harcèlement est composé : d'éléments modulés en fréquence (FME ou ABC) suivis de notes D.
Ces deux motifs (considérées comme des « mots » faisant partie intégrante de la « phrase » FME-D) peuvent être émis indépendamment l'un de l'autre.
Les notes FME correspondent à des cris d'avertissement et sont associés aux comportements de scan (tourner la tête à 180°).
Les notes D correspondent à des cris de recrutement et sont associés aux comportements d'approche.
La séquence naturelle FME-D provoque les deux réactions.
La séquence artificielle D-FME ne suscite pas d'intérêt.

Encadré 1 : Complexité des cris de harcèlement chez la mésange de Chine **(spectrogramme Suzuki et al. 2016)**

Objectifs :

Dans un premier temps, nous avons testé si la mésange charbonnière *Parus major* (espèce phylogénétiquement très proche de la mésange de Chine) utilise la syntaxe compositionnelle dans ses cris de harcèlement. Dans un deuxième temps, nous avons examiné si la mésange noire et le pinson qui répondent habituellement aux cris de la mésange charbonnière sont également sensibles à l'altération de la syntaxe.

Résultats :

- la mésange charbonnière est sensible à l'altération des motifs mais approche le haut-parleur durant la séquence artificielle (voir encadré 1).
- la mésange noire est sensible à l'altération de la syntaxe alors que le pinson ne l'est pas.

Conclusion :

Les mésanges sont sensibles à l'ordre de combinaison des motifs composants les cris de harcèlement. Cependant, cela ne veut pas dire qu'elles exploitent réellement la syntaxe compositionnelle pour transmettre plus d'informations.

Effect of compositional syntax manipulation on heterospecific response to mobbing calls

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Abstract

Harassing threatening intruders is a widespread anti-predator strategy and typically associated with mobbing calls that quickly recruit both conspecific and heterospecific prey. In Japanese tits (*Parus minor*), mobbing calls are structurally complex and have been suggested to convey information by the mean of compositional syntax (i.e., combination of meaningful motifs into a larger structure, whose meaning depends on the motifs involved and their order). Whether compositional syntax is used by other species in mobbing calls and how it can alter the ability of heterospecifics to adequately recognize mobbing calls remains unknown. To address these questions, we conducted two playback experiments. Firstly, we investigated whether the great tit (*Parus major*) extracts different meanings from different motifs alone, and from combined motifs in the natural or artificially-reversed order. We found that great tits extract different meanings from the two motifs involved in mobbing calls and that they also discriminate motif order reversion in the mobbing calls sequence. Secondly, we investigate whether heterospecifics, coal tit (*Periparus ater*) and common chaffinch (*Fringilla coelebs*), are sensitive to syntax alteration of the great tit mobbing calls. While chaffinches were not responding to great tit mobbing calls, coal tits were sensitive to mobbing calls sequence reversion although they did not react in the same way than conspecific subjects. Overall, whereas our results clearly indicate that tits are sensitive to compositional syntax, they do not well support the hypothesis that tits actually use compositional syntax to increase the information content.

Keywords: Call combination, Interspecific communication, Mobbing, Syntax, Tits

INTRODUCTION

During the last decades, accumulating evidence has revealed that animal vocalizations share several features with human language (Collier et al. 2014). In humans, the involvement of hierarchical structure in the acoustic signal enables much more information to be conveyed from a finite set of vocal elements (Berwick et al. 2013). Although animal vocalizations involve a far less complex level of organization than human language, several studies suggest that some species use at least two levels: (i) phonology, when a finite number of meaningless sounds (phonemes; i.e., syllable or note) are combined to form meaningful acoustic structures (morphemes; i.e., motif) and (ii) compositional syntax, the combination of meaningful motifs into a larger structure, whose meaning depends on the motifs involved and their order (Marler 1998; ten Cate and Okanoya 2012; Berwick et al. 2013). Although evidence for syntax becomes more and more available (e.g., Arnold & Zuberbühler 2006; Ouattara et al 2009), species ability to use compositional syntax remains debated (Petkov and Jarvis 2012; Petkov and Wilson 2012; Bolhuis et al. 2018). More recently, Suzuki et al. (2016; 2017) challenged this issue with a study of mobbing calls produced by the Japanese tit (*Parus minor*). Mobbing calls are particular forms of alarm signals widespread in animals, notably in passerine birds (Magrath et al. 2015). They are emitted by animals trying to chase away a predator and share the specific feature to prompt listeners joining the mob, a feature that often transcends species boundaries (Pettifor 1990; Hurd 1996; Dutour et al. 2017a).

Mobbing calls have been well described in Paridae (Carlson et al. 2017; Jung and Freeberg 2017) and are usually composed of combinations of frequency modulated elements (Hetrick and Sieving 2011) referred to as FME hereafter, followed by a string of a repeated loud broadband elements (Templeton et al. 2005), referred to as D notes hereafter. D notes have a large frequency bandwidth, which probably facilitates the localization of the caller and recruitment for mobbing, while the frequency modulation makes the alarm calls more difficult to localize (Marler 1955). As suggested by several authors, such a pattern could well arise from a hierarchized organization following a ‘syntactic-like’ rule (Hailman and Ficken 1986; Lucas and Freeberg 2007). In the Japanese tit, each motif alone is also involved in another context than mobbing: the FME motif is used in vigilance situations and it serves as an alarm signal to which receivers respond by scanning for danger (alert calls), while the D notes are involved in foraging flocks or in nest mates to recruit social partners and elicit an approach of the receivers (recruitment calls) (Suzuki et al. 2016; 2017). When the Japanese tits heard the FME motif combined with the D notes as the compound FME-D, also a natural vocalization, they showed both scanning and approach behaviors. However, there was little or no response when call order was artificially reversed to D-ABC. From this, authors suggest that compositional syntax basic is a mechanism of information transmission, although other alternative explanations still exist (Bolhuis et al. 2018). One may ask whether the use of a compositional syntax in mobbing calls is specific to *Parus minor* or extends to other Paridae species. Furthermore, using compositional syntax to encode information in mobbing calls from several motifs including ones involved in social cohesion with conspecifics could limit the ability of heterospecifics to correctly identify mobbing calls. This is particularly intriguing since response to mobbing calls are also well known to transcend species boundaries (Dutour et al. 2017a; Dutour et al. 2016), and one may ask whether there is actually a similar underlying compositional structure among birds species enabling them to decode information in heterospecific mobbing calls (Russell and Townsend 2017; Griesser et al. 2018).

The main objectives of the present study were first to test whether the great tit (*Parus major*), the closest relative to the Japanese tit (Johansson et al. 2013), uses compositional syntax in mobbing calls. We investigated whether receivers extract different meanings from FME or D motif alone, and from combined motifs in the natural or artificially-reversed order (i.e., FME-D or D-FME sequences). Secondly, we investigated whether heterospecifics are sensitive to syntax alteration of the great tit mobbing calls. In this second experiment, we compared responses of coal tits (*Periparus ater*) and common chaffinches (*Fringilla coelebs*) to playbacks of natural and artificially reversed great tit mobbing calls. We chose the coal tits among other Paridae species since mobbing calls of this species are particularly complex and composed of multiple motifs (Carlson et al. 2017; Dutour et al. 2017a) and also because our previous works showed that coal tits are especially prone to respond to heterospecific mobbing calls (Dutour et al. 2017a). We selected the chaffinch as an extra-group member (i.e., non Paridae species) since this species is often found in heterospecific mobs although it is less prone than tits to join heterospecific callers (Dutour et al. 2017a). Whereas mobbing calls of chaffinch were composed of a single “chink” note (Randler and Förschler 2011), we predicted that coal tits would be more sensitive to syntax alteration than chaffinches.

MATERIAL AND METHODS

Experimental design

Data were collected during playback experiments conducted at the onset of the breeding season (experiment 1, February/March 2018) and at the end of the breeding season (experiment 2, July/August 2017) on wild passerines inhabiting mixed deciduous-coniferous forests located in South-East France (45°80'N, 4°52'E). In order to examine whether great tits mobbing calls involve compositional syntax (experiment 1), we conducted five playback types. First, we examined whether each motif alone (FME calls and D calls) induced a distinct behavior, respectively vigilance and recruitment. We then examined whether tits hearing the combined motifs in the natural order (i.e., FME-D calls, natural mobbing call sequence; see audio samples in electronic supplementary material) display a combination of the behaviors they exhibit when hearing each motif alone, and we tested whether this is also the case when the combined motifs are presented in the reverse order (i.e., D-FME calls, artificially reversed mobbing call sequence). Finally we also performed control tests for which the playback contained only background noise (hereafter referred as BN tests). We conducted these tests with 100 adult great tits (20 individuals for each test type). The goal of experiment 2 was to test whether heterospecific receivers, coal tits and chaffinches, extract a compound meaning when both motifs are combined (compositional syntax) in the same way as intraspecific receivers (great tits). To this aim, we investigated how individuals of each species behave when hearing a playback of natural FME-D calls and artificially reversed D-FME calls of great tits. We also replicated these tests with great tits receivers in order to permit comparisons across species. This second experiment involved 90 different individuals (15 individuals per test and for each species).

Field test procedure

Each test was conducted by two field assistants. One of them was assigned to the soundtrack preparation and playback operation, while the other was kept unaware of the selected soundtrack and assigned to the observation of the focal bird. After the localization of a focal bird, the loudspeaker was placed 30 m away from the bird at the bottom of a tree. Both field assistants were positioned opposite each other at vantage points at least 15 m from the loudspeaker and the focal bird to avoid any perturbation during the test. Before the beginning of the experiment, the baseline behavior of the focal bird was observed during at least 1 min pre-trial period. If the bird was found to show alarm behavior (i.e., emit mobbing calls, less than 5% of the cases) the test was abandoned. Otherwise, the playback was started when there was no other passerine observed near the focal individual. Then, during 1 min of playbacks, two behavioral variables were recorded to infer vigilance effort and recruitment propensity, respectively (1) the number of horizontal scans (we counted the number of movements that birds made with their heads from left to right or right to left (approximately a 180 turn);

Suzuki et al. 2016) and (2) the approach within a radius of 15 m from the loudspeaker (Dutour et al. 2017a). All observations were done using binoculars and the congruence of the data recorded by each field assistant was controlled although only those collected by the one unaware of the soundtrack used was conserved. Thus, to minimize observer bias, blinded methods were use when all behavioral data were recorded. Data on scanning behavior were collected mainly by one observer using binoculars. All trials were conducted between 06:00 and 13:00 h during calm and dry weather. All focal animals were selected to be always separated by more than 100 m to minimize pseudo-replication risk. In addition, we never went back twice on the same forest path and during the breeding season tits territories are separated by 50 m. Once a test was done, we went at more than 100m before trying to detect another bird having a calling or a foraging activity. No bird was seen following us. Hence, although birds were not individually ringed, the probability of testing the same individual twice was low and we are confident that our observations were performed on different individuals. Moreover, playback sequences were evenly distributed across the study period to avoid any temporal confounding effect (Dutour et al. 2017a).

Playback stimuli and playback materials

We used mobbing calls produced by three great tits previously recorded in response to intraspecific mobbing calls (Dutour et al. 2017a). Calls were recorded with a Fostex FR2LE digital recorder connected to a Sennheiser ME67-K6 microphone (see Dutour et al., 2017a for more details). We also used mobbing calls obtained from the Xeno Canto online database (www.xeno-canto.org) recorded in different European countries (n =7) located along the species' range in order to encompass the call variation range that a local bird community could experience and to generalize our conclusions. From these recording files, we built 20 unique soundtracks of natural mobbing calls (FME-D sequence) using Avisoft-SASLab software (i.e., 20 soundtracks with 1 individual per soundtrack). These soundtracks were then used to construct three other ones, respectively FME calls, D calls, and D-FME calls as follows: FME and D calls were constructed by removing either D or FME calls from each FME-D calls and the D-FME calls were constructed by reversing the motifs order of the original FME-D calls of great tits (Fig. 1). Within each sound track, calls were repeated at a rate of 26 calls per minute (this calling rate is within the range of the natural repetition rates, unpubl. data). We used a series of five to eight D motifs to construct playback (mean ± s.e. = 7.11 ± 0.06; Fig. 1s). Each track D notes were placed 82 ± 40 ms before FME (no difference with time between FME and D notes in the natural sequence; t = 1.789, p >0.05). The number of D notes could relate to the perceived level of threat (Templeton et al. 2005) which could artificially entail variation in the response of focal birds. For this purpose, all playback sequences were arranged to adjust the ratio of the D notes over the FME ones in a mobbing call sequence making this ratio slightly lower in our study (range: 5/8 - 8/11) than in Suzuki et al. (2016, range: 7/10 - 10/13, see Fig. 1 in both ms for comparison). We also constructed 20 control soundtracks using the parts where no birds were calling in the same recordings as natural mobbing calls (BN). In order to avoid pseudoreplication (Kroodsma et al. 2001), we played back each soundtrack only once using a Shopinnov 20 W loudspeaker (the probability of testing an individual twice was low, see above). The sequence was emitted with an intensity of 75 dB(A) (measured at 1 m from the loudspeaker using Lutron SL-4001, C weighting, slow settings, re: 20 m Pa).

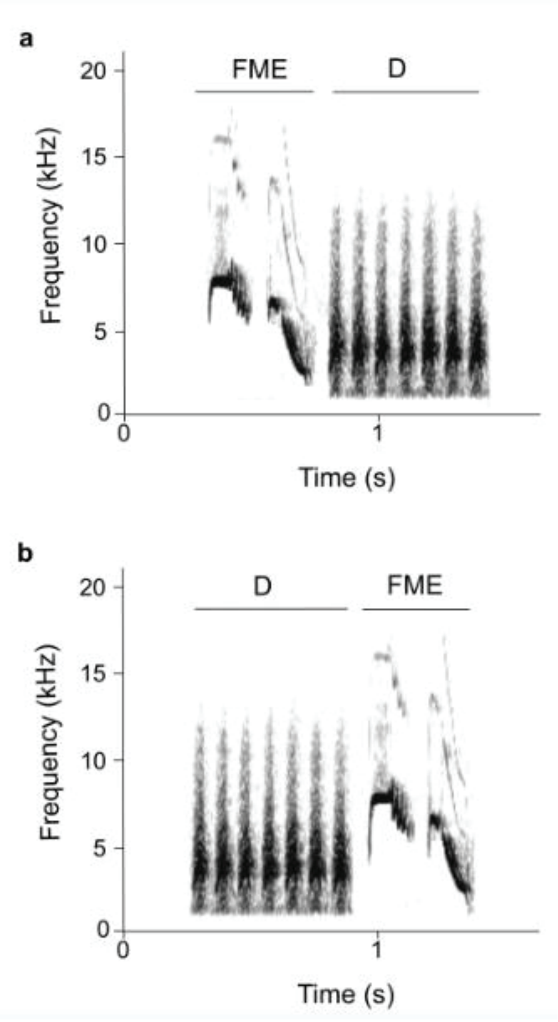

Fig. 1 Spectrograms of calls played to great tit, coal tit and chaffinch: **a** FME-D mobbing call of the great tit showing call with introductory frequency modulated elements (FME) (similar to chickadee A or B elements) and subsequent D notes (D) and **b** D-FME call is a reversed combination of FME-D calls. These calls were produced with Avisoft SASLab©

Data analysis

In the analysis of experiment 1, we used generalized linear models (GLM) including the test type (FME calls, D calls, FME-D calls, D-FME calls and control) as an explanatory term. For the analysis of horizontal scans, we used a negative binomial error distribution and log-link function (*glm.nb*, package MASS) and treated the observation duration (i.e., the time during which we could observe the bird) as an adjustment covariate. For the approaching behavior, the individual binary response (i.e., approaching versus no approaching) was introduced as the dependent variable using a logit link and a binomial distribution for the error term (*glm*). For both response variables, multiple comparisons between test types were performed with Tukey correction (*glht*, package multcomp). Finally, for each test type, we used a Wilcoxon test to determine whether scanning differed between approaching individuals and those staying away or conversely whether each approach was associated with scanning. Tests were not performed for the FME and the BN playbacks given the lack of approaching bird in these treatments (see Results).

We proceeded in a similar way for the analyses of experiment 2. We first verified that the mobbing call sequence reversion resulted in the same behavioral pattern for conspecific receivers as observed in experiment 1. More specifically, we compared the number of scans and propensity to approach using GLMs including the test type as an explanatory term. Period (the onset of the breeding season (i.e., experiment 1) or the end of the breeding season (i.e., experiment 2)) was also entered as covariate. We then compared the response of the three species to the great tits mobbing calls presented in the natural order (i.e., FME-D calls). For this purpose, the receiver species (great tit, coal tit and chaffinch) was introduced as an explanatory term in the models for the two behaviors (scan and approach). We then performed separate analyses for each receiver species, to test the difference in response according to the mobbing call sequence reversion. Because none of the coal tits approached when exposed to the reversed sequence (i.e., D-FME calls; n = 15), it was not possible to include this test type in a parametric analysis. We therefore used a Fisher exact test to compare the approaching propensity between FME-D and D-FME sequences. We also completed these analyses by Wilcoxon tests to investigate for each species the relationship between vigilance and approach within each test type (i.e., FME-D and D-FME sequences). These tests were not performed for coal tit in response to D-FME sequence since no individual approached during the test and no for chaffinches since almost none individual approached during the test (see Results). All analyses were done in R v.2.15.1.

RESULTS

Experiment 1: compositional syntax in great tit mobbing calls

Overall, our analyses indicate that scanning behavior significantly varied according to the test type ($n = 100$, $\chi^2 = 64.85$; $df = 4$; $P < 0.0001$; Fig. 2a). The pairwise comparisons between D calls, D-FME calls or control tests were non significant (all $P > 0.05$) as well as the comparison between the FME calls and FME-D calls tests ($z = -1.48$, $P = 0.57$). However, both FME and FME-D calls were associated with significantly more scans that the D calls, D-FME calls or control tests (all $p < 0.001$).

The probability of approaching significantly varied between the test types (generalized linear model: $\chi^2 = 29.97$; $df = 4$; $P < 0.0001$; Fig. 2b). In response to D calls, great tits were more likely to approach the loudspeaker than in response to FME calls ($z = 3.16$; $P = 0.012$) and control ($z = 3.16$; $P = 0.012$) whereas there was no significant difference between D, FME-D and D-FME calls (all $P > 0.05$). Tits were also more likely to approach the loudspeaker during the FME-D calls than in response to FME calls ($z = 2.63$; $P = 0.05$) and control ($z = -2.63$; $P = 0.05$). Finally, regardless the test type, we did not find any significant correlation between horizontal scanning and approaching behavior (Wilcoxon test for the D, FME-D, D-FME playback treatment: all $P > 0.05$; test not performed for the FME and the BN playbacks given the lack of approaching bird in these treatments).

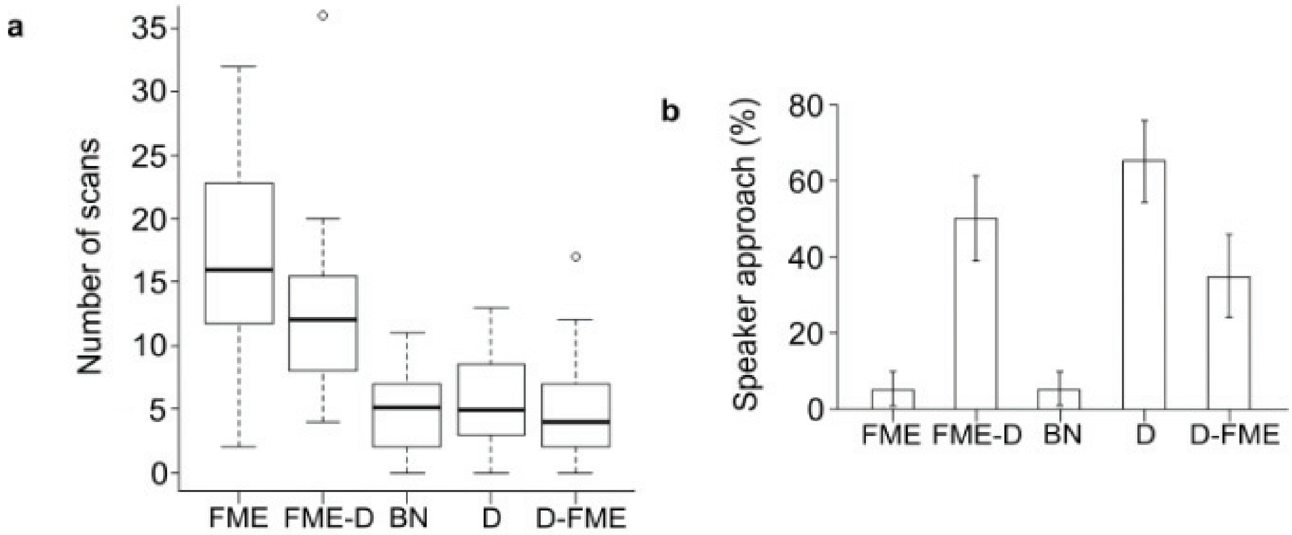

Fig. 2 Responses of great tits to playbacks of FME, FME–D, control (BN), D and D–FME test types. **a** Number of scans made by tits during playback. Horizontal line: median value; box ends: upper and lower quartiles; whiskers: variation range of values. **b** Percentage of trials in which tits approached the loudspeaker;

Experiment 2: effect of syntax alteration on heterospecific perception

There was no significant difference between periods (before and after reproduction) neither in horizontal scans ($\chi^2 = 2.69;\ df = 1;\ P = 0.10$) nor approaching behavior ($\chi^2 = 0.83;\ df = 1;\ P = 0.36$). As in experiment 1, great tits still approached the loudspeaker with the same propensity ($\chi^2 = 0.54;\ df = 1; P = 0.46$; Fig. 3a) but significantly reduced their vigilance effort ($\chi^2 = 18.2;\ df = 1; P < 0.0001$; Fig. 3a) when hearing conspecific mobbing calls in the reversed order rather than in the natural order. Similarly to experiment 1, the number of scans was also not significantly influenced by the propensity to approach the loudspeaker (Wilcoxon test respectively for the FME-D and the D-FME sequence: n = 15, W = 29; P = 0.86; n = 15, W =25; P = 0.77). These results indicate that the magnitude of subject's reaction to conspecific calls remained unchanged before and after reproduction and offers stable ground for interspecific comparison.

Among the other two species, the chaffinches showed a very low scanning activity and rarely approached the emitter regardless the sequence order (Fig. 3c). This species was therefore discarded for future analyses. In contrast, the coal tits displayed both a vigilance effort as well as a propensity to approach the emitter approximately equivalent to great tits receiver when hearing the FME-D sequence (test for difference between species respectively for the scanning activity and the propensity to approach: z = -1.19, P = 0.23 ; z = -1.45, P = 0.15, Fig. 3a). Listening to a reverse sequence, coal tits displayed both a significantly reduced vigilance effort ($\chi^2_1 = 8.08, P = 0.005$) and a reduced propensity to approach the loudspeaker (Fisher test: $P = 0.042$) (Fig. 3b). Moreover, contrarily to the great tits, coal tits approaching the loudspeaker also scanned significantly more intensely (14.2 ± 3.9) than those staying away (8.1 ± 5.2) when hearing the great tits mobbing calls in the natural order (Wilcoxon test: n = 15; W = 8; P = 0.042, test not performed for the D-FME sequence given the lack of approaching bird in this treatment).

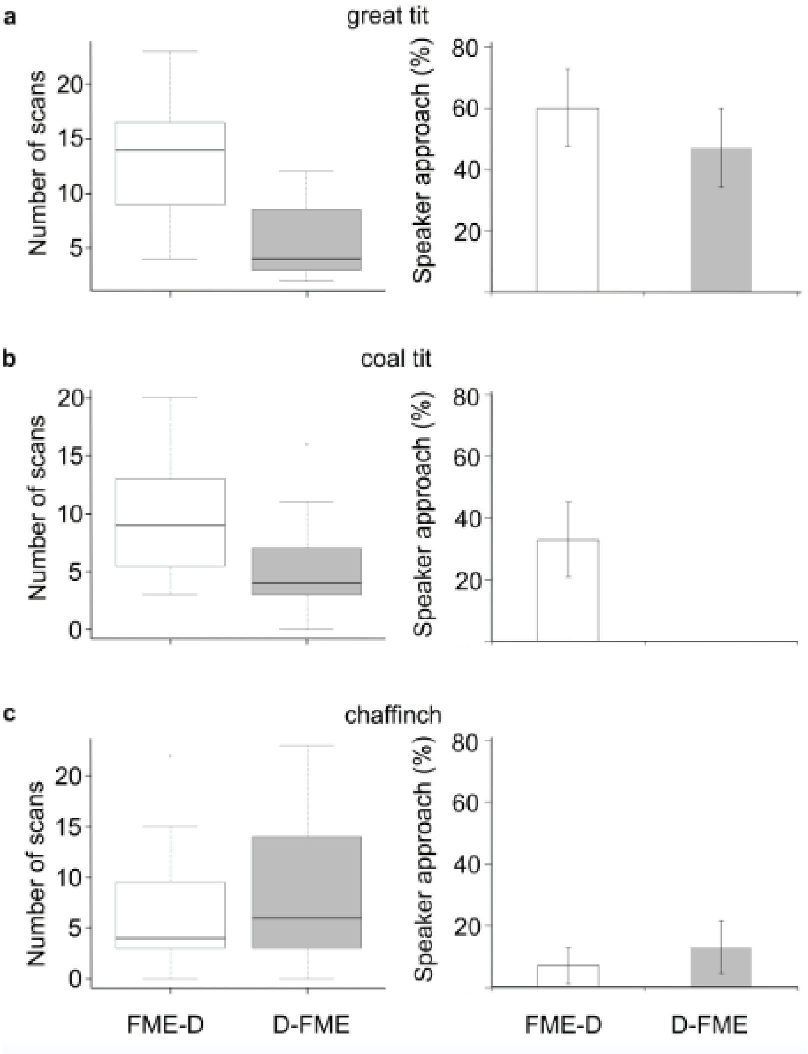

Fig. 3 Number of horizontal scans and percentage of trials in which **a** great tits, **b** coal tits and **c** chaffinches approached the loudspeaker during the presentations of the playbacks of FME–D and artificially reversed D–FME motifs of mobbing signals. Horizontal line: median value; box ends: upper and lower quartiles; whiskers: variation range of values

DISCUSSION

We found that great tits behave distinctly when hearing respectively the FME motifs and the D ones: they scan the environment when hearing the former, and approach the sound source when hearing the latter ones. As previously evidenced in the Japanese tits (Suzuki et al. 2016; Suzuki et al. 2017), these results indicate that these two motifs also convey distinct meanings in the great tit, one corresponds to an alarm call (i.e., the FME motif) which elicits vigilance effort from the receiver, while the other corresponds to a recruitment call (i.e., the D motif) which elicits an approach behavior from the receiver. These findings are also well congruent with the acoustic properties of each motif, since the frequency modulation makes the alarm calls more difficult to localize while large frequency bandwidths make the recruitment calls easily localizable (Marler 1955; Shalter 1978; Klump 2000) (in the present study; frequency bandwidth = differences in Hz between maximum frequency and minimum frequency measure on a linear amplitude spectrum; threshold -20dB; using Avisoft-SaSLab; mean ± SE respectively FME calls and D calls: 2894 ± 485 Hz; 7437 ± 788 Hz). These results relate also to the motivation-structural hypothesis suggesting that sounds emitted by birds and mammals in aggressive or hostile circumstances should be wide bandwidth and low-frequency, whereas sounds given in a fearful context should be high-frequency (Morton 1977; Angust and Anderson 1987). Great tits exhibited both an increased vigilance effort (high proportion of scanning) and a rapid approach (*n* =19; mean ± SE = 30.22 ± 3.38 seconds) toward the emitter when hearing the naturally ordered mobbing calls sequence (i.e., FME-D calls), indicating that tits extracted both meanings from the naturally ordered combination of the two motifs. Both the nature and the magnitude of the responses we observed in the present study are very similar to those obtained on the Japanese tit (Suzuki et al. 2016). However, while in the Japanese tits both the vigilance effort and the propensity to approach vanish when tits hear the mobbing call sequence in the reversed order (Suzuki et al. 2016; Suzuki et al. 2017), the results are markedly different in the case of the great tit: the vigilance effort vanishes but the propensity to approach is kept constant when the combination order is reversed. Since we observed similar responses in both experiments which were performed in two breeding seasons, this behavioral pattern is well reproducible. Our results therefore suggest that great tits are sensitive to the ordered combination of the two motifs. However, as noted by several authors (ten Cate and Okanoya 2012; Berwick et al. 2013), this is not to say that tits actually exploit compositional syntax to convey more information. To our knowledge, great tits never use reversed mobbing calls sequences in the wild, and three alternative hypotheses could explain a sequence order reversion effect without invoking compositional syntax usage.

First, these results could be explained by the occurrence of a perception bias (Klump & Gerhardt, 1992; Grafe, 1996) when the sequence order is reversed. Indeed, D notes, which are large frequency bandwidths enhancing location, may operate as auditory masking on the FME notes (frequency modulations resistant to degradation; Marler, 1955; Brown & Handford, 1996) given the relative short delay between both sequences. Thus tits could no longer perceive the FME notes when they are artificially placed after the D notes. Such a phenomenon could well explain why great tits reduced vigilance behavior when hearing the artificially reversed sequence of mobbing calls. Secondly, as highlighted by Bolhuis et al (2018), to tit receivers, first scanning and then approaching may well be a more adaptive response order than the other way around. Upon predator detection, it is unlikely that the behavioral sequence is irrelevant. Receivers are not expected to carry out maladaptive response sequences, even if they interpret the signal as carrying such a meaning. Consequently, it may be maladaptive for emitters to produce such signals, which is why they are not found. Finally, without previous learning, unnatural ordering of the mobbing calls sequence could result in receiver misinterpretation or misconception of the conveyed information. Indeed, tutors often play a central role in bird vocal learning (Brainard and Doupe 2013) and associative learning is also involved in mobbing behavior (Magrath et al. 2015; Brainard and Doupe 2013). Mobbing call responsiveness (and or interpretation) may also depend on the social context, for instance according to the presence of the receiver's mate in the vicinity (Suzuki et al. 2016) or the seasonal activity (Lucas et al. 2007; Dutour et al. 2017b). In the Japanese tit, the sequence reversion effect was examined in flock members during the non-breeding season (Suzuki et al. 2016), whereas tests were conducted on territorial individuals in the great tit (i.e., the present study). Since the sensitivity to recruitment calls may vary between these two social contexts, further work is required to examine this point.

Chaffinches were barely sensitive to great tit mobbing calls although this species is regularly observed in heterospecific mobbing groups (Dutour et al. 2016). Moreover, we recently found a very low responsiveness of chaffinches to heterospecific mobbing calls when compared to their own mobbing calls (Dutour et al. 2017a). We suggested that such lack of response could be explained by a strong dissimilarity between mobbing calls of the chaffinch and other species. There are other possibilities to explain these results, such as the exploitation of a distinct ecological niche. Such a hypothesis cannot explain our results because chaffinches and great tits usually share the same ecological niche. It is therefore likely chaffinches sensitive to their own species only although the absence of a background noise test in experiment 2 cannot allow us to safely conclude on this point.

Conversely, coal tits were not significantly less responsive than conspecific subjects to the naturally ordered great tit mobbing calls sequence (i.e., FME-D sequence) regardless of the measured behavior (i.e., vigilance or approach). However, their behavior markedly differ from that of conspecific great tit subjects since approaching coal tits were also more vigilant than those staying away, whereas approaching great tits were not significantly more vigilant than their counterparts staying away. Furthermore, and above all, when the mobbing call sequence order was reversed, coal tits not only reduced their vigilance effort but they also no longer approached the emitter. If these results clearly indicate that coal tits are particularly sensitive to great tits mobbing call sequence reversion, they also strongly suggest that coal tits do not extract the same meaning from the mobbing calls sequence as great tits do. In particular, their responsiveness seems more binary or less versatile than that of the one of great tits. This could indicate that some information (i.e., social information) is present in great tits mobbing calls and induce conspecific responses while coal tits do not pay attention to it. One additional hypothesis could be used to explain the behavior of coal tits: it is possible that coal tits acquire the meaning of FME, D and FME-D sequences via associative learning because these signals can be heard repeatedly in the field. In contrast, coal tits cannot have acquired any 'meaning' for D-FME sequences as they are never uttered. This may explain their lack of reaction to these stimuli. This hypothesis would also be consistent with the 'correlation' between scanning and approach in coal tits (i.e., the binary response depending on whether the birds have been exposed enough to great tits to associate these calls with a danger, or not). Additional playbacks to verify coal tits' and chaffinches' reactions to FME and D notes, as well as to artificial stimuli starting with and FME- or a D- motif (but finishing with another motif that is normally not used in combination with these motifs) would be most valuable to disentangle this question.

Our results also suggest that the combination order of the repetitive loud and broadband notes (i.e., the D motif) preceded by the frequency modulation notes (i.e., the FME motif) within the mobbing calls sequence is of prime importance to elicit a response in the receiver, especially for heterospecific ones. In this respect, it is particularly striking that, in the few bird species for which the effect of compositional syntax has been investigated, all studies reported that natural mobbing call sequences follow this combination ordering (Templeton et al. 2005; Suzuki et al. 2016; Suzuki et al. 2017). Furthermore, as suggested by the present study and recent studies on the Japanese tit (Suzuki et al. 2017), it seems that this rule is more important than the acoustic similarity of each motif between species to enable heterospecific response. Nevertheless, whether this rule applies more broadly to bird communities remains to be established and further studies on a larger set of bird species should be done. Furthermore, as birds may not only eavesdrop on heterospecific communication to extract information about predator threats but also about food resources (Magrath et al. 2015), future work is needed to clarify how each motif alone (i.e., alert calls and recruitment calls) is understood by heterospecifics.

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Chapitre 3

Rôle de l'Apprentissage dans la Mise en Place de la Réponse aux Signaux de Harcèlement

<u>Article 7</u> : Mobbing in great tit (*Parus major*) : the implication of associative learning process

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Animal Behaviour, resoumis septembre 2018

Problématique :

De nombreuses espèces obtiennent des informations sur la présence d'un danger en écoutant les cris de harcèlement. Si le harcèlement a beaucoup été étudié chez les adultes de nombreuses espèces, on ne sait pas comment la reconnaissance des cris de harcèlement se met en place. L'apprentissage associatif est-il un mécanisme impliqué dans le développement de la reconnaissance des signaux de harcèlement chez les poussins de mésange charbonnière *Parus major* alors qu'ils sont encore dans le nichoir ?

Objectif :

Nous avons étudié si l'expérience d'un stimulus non familier associé à des cris de harcèlement conspécifiques et diffusé pendant toute la période de développement permettait aux jeunes d'associer ce stimulus non familier à un comportement de harcèlement après l'envol.

Résultats :

- les réponses comportementales et physiologiques des poussins dans le nichoir ne varient pas selon qu'ils aient entendu le signal associé à des cris de harcèlement ou un signal neutre.
- après l'envol, les jeunes soumis aux cris de harcèlement répondent plus au stimulus non familier que les jeunes soumis au signal neutre.
- le comportement des jeunes soumis aux cris de harcèlement est perturbé lorsqu'ils sont confrontés à des cris de harcèlement.

Conclusion :

Cette étude permet de mettre en évidence que les jeunes apprennent à associer un stimulus non familier avec des cris de harcèlement et présentent des comportements de vigilance en réponse au stimulus non familier alors qu'ils n'en étaient pas capables lorsqu'ils étaient dans le nichoir.

Mobbing in great tit (*Parus major*):
the implication of associative learning process

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Abstract

Many animals gain information about the presence of a threat by listening to alarm calls. In some cases, prey emit mobbing calls, which are associated with the caller approaching and harassing the predator while encouraging others to join it. Surprisingly, although mobbing has been widely reported in adults of numerous species, how mobbing call recognition take place remains largely unexplored. Here, we trained wild great tit, *Parus major*, nestlings by playing back an unthreatening, novel sound either associated with an acoustic functional stimulus (i.e. conspecific mobbing calls; associative learning treatment) or with another unthreatening, novel sound (control treatment). We then tested them as nestlings and fledglings to see how response to the novel sound compared to actual conspecific mobbing calls. Results reveal that fledglings in the associative learning treatment behaved similarly to conspecific mobbing calls and the novel sound associated with conspecific mobbing calls. Because mobbing is often linked to interspecific communication, associative learning could be used by heterospecifics as a mobbing calls recognition mechanism. Regardless of treatment group during the nestling phase, fledglings always were sensitive to the playback of conspecific mobbing calls. However, only fledglings from the control group were more likely to approach when played the mobbing calls suggesting that reinforcement during the nestling phase altered mobbing learning. Overall, these results suggest therefore that the learning process plays a central role in the recognition of mobbing calls but that call overexposure during the nestling phase may prevent fledglings from expressing the complete mobbing behavioural chain.

Key words: alarm call, associative learning, birds, communication, mobbing, *Parus major*

INTRODUCTION

In numerous species of small birds and mammals, two contrasted anti-predator strategies, each associated to a specific alarm call, are observed according to the predator dangerousness: prey may flee or mob the predator (Marler, 1957). Mobbing behaviour is usually exhibited when predators do not represent an immediate threat and is characterized by both repetitive attacks on the predator and vocalizations (i.e. mobbing calls) that quickly gather neighboring counterparts as well as other prey species in the mob (Curio, 1978; Hartley, 1950). Both the evaluation of the threat associated to the predator and the recognition of mobbing calls, including heterospecific ones, are required to make mobbing behaviour an efficient anti-predator strategy.

Associative learning is a behavioural modification following reinforcement, based on associations between two stimuli, responses or events (Griffin, Healy, Guillette, 2015; Shettleworth 1998). This process is essential to the development of vocalization and several behaviours such as those involved in predator avoidance (Ferrari & Chivers, 2011). Animals can learn to flee after associating a unfamiliar sound (i.e. novel sound) with (i) the appearance of a model predator (birds: Magrath, Haff, McLachlan, & Igic, 2015a; mammals: Shriner, 1999) or (ii) with known alarm calls, without having to see the callers or a predator (Potvin, Ratnayake, Radford, & Magrath, 2018). In mobbing behaviour, a process of associative social learning has been found between conspecific mobbing calls and predators (Curio, Ernst, & Vieth, 1978a; Maloney & McLean, 1995; McIvor, Lee, & Thornton, 2018; McLean, Hoelzer, & Studholme, 1995), but in all cases the training phase was based on visual cues. However, a visual associative learning needs the inexperienced learner to be in the vicinity of the mobbing scene, so that the opportunities for learning while reducing the risk of threat may be limited, especially for species living in dense vegetation. This is not the case of acoustic-acoustic association that may be efficient even when the tutor and the threat are difficult to observe, an associative learning that could result in the rapid spread of mobbing call recognition in natural communities.

Evidence from both laboratory studies and field experiments suggests that learning plays an important role in the recognition of predators (Curio, Ernst, & Vieth, 1978b; Campbell & Snowdon, 2009; Davies & Welbergen, 2009; Dutour, Lena & Lengagne, 2017a). Furthermore, response to mobbing calls is based on both learning and innate components (Randler 2012; Wheatcroft and Price 2013; Dutour et al. 2017b). Mobbing calls are usually characterized by loud and repetitive vocalizations, both features that should facilitate associative learning, as there is ample opportunity to listen mobbing calls while observing the threat, and probably little danger to do so (Magrath et al. 2015b). In birds, such association between a predator and the expression of a mobbing behaviour could be achieve by the time chicks fledge. In this case, parents play the role of tutor and several observations are in agreement with this statement (Curio, Ernst, & Vieth, 1978b; Griesser & Suzuki, 2016). But, if nestlings are able to associate several acoustic signals from their nestboxes, they can also express a mobbing behaviour as soon as they leave the nest. To our knowledge, this capacity has never been investigated before.

Great tit, *Parus major*, is a well-suited species to study the ontogeny of mobbing behaviour in the wild. It is well known for its learning abilities (Cole, Cram, & Quinn, 2011; Exnerová et al., 2006; Morand-Ferron, Hamblin, Cole, Aplin, Quinn, 2015) and is known to exhibit mobbing behaviour and emit mobbing calls when confronted with a predator (Carlson et al. 2017a; Dutour, Lena, & Lengagne, 2016; Lind et al., 2005). Furthermore, this altricial species provides a good system for studying whether naïve nestlings are able to associate mobbing calls with neutral stimuli in the absence of any visual cues from adults or predators in the nest cavity.

The goal of this study was to determine whether associative learning might serve as a mechanism for the development of mobbing calls recognition for free-living animals. Specifically, we investigated whether experiencing a novel stimulus associated with conspecific mobbing calls during the nestling period led great tit nestlings to associate this novel sound with mobbing during the fledgling period. We designed playback experiments in two groups: (i) an associative learning group in which we trained individuals by broadcasting a novel sound (i.e. associative learning stimulus) with mobbing calls (i.e. functional stimulus) and (ii) a control group in which the associative learning stimulus was broadcast with another novel sound (hereafter control stimulus).

At the end of the learning period, in line with previous work showing that nestlings cease begging when they hear playbacks of their parents' alarm calls (Hollén & Radford, 2009), we predicted that only associative learning nestlings should cease begging when they heard the associative learning stimulus. We also measured the hormonal responses of nestlings. Under the hypothesis that earing parental mobbing calls is a stress for nestlings, in the late-stage nestlings, we predicted a higher corticosterone level for nestlings of the associative learning group due to the daily perception of mobbing. Moreover, under the hypothesis that nestlings associate mobbing calls with associative learning stimulus, we expect that these birds emphasized a higher corticosterone level when earing associative learning stimulus than control birds. We also measured responses at the fledgling stage after the playback of associative learning stimulus. We predicted that the playback of associative learning stimulus would elicit a stronger mobbing response from associative learning fledglings compared to control ones (i.e. increases in scanning, calling and moving). Because it was important to ensure that fledglings are able to mob, we also tested whether they responded to the playback of conspecific mobbing calls.

MATERIAL AND METHODS

Study sites and species

We chose great tits, a common monogamous territorial passerine, which breeds in secondary holes and wooden artificial nest-boxes throughout Europe and parts of Asia and North Africa (Perrins, 1965). The study was conducted in the Pierre Vérots Foundation, a private natural reserve located in the south-east France (4°55'030"E, 45°57'N). The study area covers approximately 150 ha which contains 120 nest-boxes separated at minimum by 50 m and mainly occupied by great tit. This distance corresponds to the minimum distance separating tits territories during the breeding season in our study area and is far enough to avoid that the playbacks are spatially dependent (at 50 meters, the amplitude levels fluctuate from 33 to 39 dB, obtained from the loudspeaker, Solo 01dB Metravib, Z weighting, re: 20 µ m Pa; these levels are lower than the natural background noise levels in forest areas, fluctuate from 35 to 45 dB in quite situation, 52 to 70 dB in noisy situation). The study took place during the breeding season (April-July 2017). We visited nest boxes every two days at minimum from the beginning of the breeding season onwards to determine the laying and hatching dates. When the nestlings were 8 days old, they were ringed with a unique combination of color bands for individual identification. Nestlings spent 19.3 ± 1.4 days in the nest. Young from the same nest hatched on the same day and subsequently also fledged on the same day as one another.

Experimental procedures: presentation of stimuli

The aim of our experiment was to assess whether chicks were able to associate a novel stimulus with conspecific mobbing calls. In 120 nest boxes, 31 were not occupied, 14 occupied by the blue tit, *Cyanistes caeruleus*, and 1 occupied by the willow tit, *Poecile montanus*. Each of the 74 nest boxes occupied by great tits was randomly assigned to one of the two treatments (balanced for laying date to ensure equal representation of both treatment groups over the breeding season). In the first treatment (38 nests), the associative learning stimulus was associated with conspecific mobbing calls (hereafter associative learning group) while in the second treatment (36 nests) the associative learning stimulus was associated with neutral stimulus (control sequence, hereafter control group). Behavioural tests were conducted both during the development of nestlings and the fledging day. Playbacks were always broadcasted once adults were silent and away from the nest (at least 15 m) or from the focal fledgling (at least 5 m).

Choice of experimental stimuli and playback materials

Three kinds of stimuli were used during playback experiments. First, we used mobbing calls produced by four great tits in response to an Eurasian pygmy owl, *Glaucidium passerinum*, and to conspecific mobbing calls. Calls were recorded with a Fostex FR2LE digital recorder connected to a Sennheiser ME67-K6P microphone. We also used mobbing calls produced by ten great tits obtained from the Xeno Canto online database (http://www.xeno-canto.org) (see Appendix 1). Then, concerning the associative learning and the neutral stimulus, we used two musical instrument sounds (clarinet and trumpet sequences) obtained from an online sound bank (http://www.universal-soundbank.com) to ensure the stimuli used had no biological value. We matched the frequency characteristics and temporal structure of the associative learning and the neutral stimulus to obtain stimuli of the same duration and the same frequency bandwith using Avisoft-SASLab Pro. For the associative learning treatment, we built playbacks containing associative learning stimulus (i.e. clarinet) with mobbing calls. For the control treatment, associative learning stimulus was associated with the neutral stimulus (i.e. trumpet) (spectrograms of mobbing calls, associative learning stimulus and neutral stimulus are available on supplementary material Appendix 2 Fig. A2). In order to avoid habituation of playbacks, we constructed 21 1 minute playback samples for each group and each sample was used only once (i.e. nestlings spent 19.3 ± 1.4 days in the nest, we used one stimulus by day) (Hurlbert, 1984; Kroodsma et al., 2001). We used mobbing calls produced by 14 great tits in total to construct 21 different playback sequences. Thus, it is right that some soundtracks are only imperfectly independent from other ones, but the risk of pseudoreplication is clearly minimized and could not itself explain our results. We also built two other 30 seconds playback samples containing associative learning stimulus or mobbing calls. The average amplitude used for these playbacks was obtained with a sound level meter placed 1 m from the loudspeaker (83.9 ± 3.51 dB, mean ± SD, Solo 01dB Metravib, Z weighting, re: 20 µ m Pa). We broadcast sound tracks using a Shopinnov 20 W loudspeaker (frequency response 100 Hz -15 kHz).

Behavioural responses of nestlings

Call suppression is described as a good measure of whether nestlings interpret sounds as cues of danger (Magrath, Haff, Horn, & Leonard, 2010). To determine whether playback treatment (i.e. associative learning stimulus with neutral stimulus or associative learning stimulus with mobbing calls) influenced nestling calling activity, every day between hatching day and flying day, we studied begging call propensity within the nest box during 30 s (begging call = 1, no begging call = 0) before and after broadcasting the treatment. More precisely, it was easy to hear begging calls near the nest and one observer came near it to determine the call propensity. The presence of observer did not impact the call propensity. Although they were multiple observers we did not detect an observer effect ($P > 0.05$). Additionally, at the end of the nestling phase, begging call propensity was measured before and after playback of associative learning stimulus. To create a natural situation as possible, the loudspeaker was placed on the top of the nest-box. In the field, the amplitude of mobbing calls of parents has not been measured accurately before (i.e. the precise distance between the bird and the sound level meter taking the exact position of the head of the bird into account). Hence, we decided to match by ear the amplitude of the calls used during our test to a natural call produced by passerines while mobbing. In the nestboxes, the average amplitude used for the playback was obtained with a sound level meter placed in the nestboxes (67.98 ± 0.94 dB, mean ± SD, Solo 01dB Metravib Z weighting, re: 20 µ m Pa).

Stress level of nestlings

Corticosterone, which is the most common hormone used to determine stress level in birds (e.g. Romero & Romero, 2002; Stöwe, Rosivall, Drent, & Möstl, 2010), was analyzed from saliva samples using ELISA test (enzyme-linked immunosorbent assay) previously validated for animal glucocorticoids detection (Janin, Léna, Deblois, & Joly, 2012; Sheriff et al., 2011). Saliva samples were collected from 100 nestlings (from 10 nests, 5 nests per treatment group; 10 nestlings per nest) at two different ages: when nestlings were 13 days old to measure baseline corticosterone level and when nestlings were 15 days old five minutes after the end of the associative learning stimulus playback. Briefly, a cotton ball was directly introduced into a nestling's mouth for 15 s. The time of handling and saliva sampling for one nestling did not exceed 1 minute. Each cotton ball was weighed before and after sampling saliva, to deduct the amount of saliva.

Samples were reconstituted by addition of 150 μL of phosphate buffer (1 M phosphate solution containing 1% bovine serum albumin, 4 M sodium chloride, 10 mM ethylenediaminetetraacetic acid, and 0.1% sodium azide) and centrifuged at 8000 rpm for 5 min at room temperature. Sample were diluted further and used for corticosterone analysis, which was carried out in duplicate with a colometric 96-well ELISA kit (number 501320, Cayman Chemical, Ann Arbor, Michigan). This method is based on the competition between corticosterone and a corticosterone –acetylcholinesterase conjugate for a limited number of corticosterone polyclonal antiserum binding sites. The color reaction was developed using Ellman's reagent containing acetylthiocholine and 5,5′-dithio-*bis*- (2-nitrobenzoic acid). The concentration of corticosterone in saliva samples run in duplicate was calculated using a standard curve run on each plate. The intensity of the color, evaluated using a spectrophotometer (Absorbance Microplate Reader ELx808, Biotek) at 405 nm wavelength, is proportional to the amount of corticosterone–acetylcholinesterase conjugate bound to the well, which is inversely proportional to the amount of free corticosterone present in the sample. We estimated the corticosterone concentration in 1 mg of saliva by dividing the measurement in the samples by the amount of collected saliva. The assay detection limit was 20.5 pg/mL. We mixed the nestlings' saliva from the same nest to assess the mean corticosterone level per brood. In addition, this pool of saliva allowed us to avoid the assay detection limit (20.5 pg/mL), thus guaranteeing high accuracy in the analyses.

Behavioural responses of fledglings

To test whether associative learning is involved in the development of mobbing calls recognition, we studied fledglings' responses to the playback of either the associative learning stimulus alone (control: N = 30 from 22 nests; associative learning: N = 31 from 19 nests) or the conspecific mobbing calls (control: N = 19 from 14 nests; associative learning: N = 26 from 16 nests). Tests were performed during the fledging day (except 4 tests conducted the second day after fledging corresponding to 3.8% of total tests). In all experiments and before the playback, the identity of the focal fledgling was determined using the unique leg color bands fitted to each fledgling using binoculars. Once a focal fledging was identified, the loudspeaker used to broadcast the acoustic stimulus was placed ~ 20 m from the bird. Data were collected mainly by one observer using binoculars. Observations were made ~10 m from the tree with the loudspeaker. All trials were conducted on average around noon (range

8:00 -17:00 h) during calm and dry weather. Playbacks were started when no birds were visible around the speaker tree and no birds were calling. Newly fledged tits had poor motor skills after they left the nest. All young of the same nest spend most of the day sitting high up on the same tree (personal observations). To test the fledgling's responses, we recorded the following behavioural variables during the 30 s of playbacks: (i) number of horizontal scans (i.e. the number of movements that birds made with their heads from left to right or right to left), (ii) mobbing vocalizations (call propensity: mobbing vocalization = 1; no mobbing vocalization = 0), (iii) approaching the loudspeaker (i.e. we recorded whether birds approached within 15 m of the loudspeaker during the playback; see Dutour, Léna, & Lengagne, 2017b for more details) and (iv) fleeing (i.e. we recorded whether birds fled more than 10 m from their initial position). We measured these behaviours because they are used as indicators of perceived danger in birds (Curio, Ernst, & Vieth, 1978a) and are common during mobbing events (Carlson, Healy, & Templeton, 2017a; Carlson, Pargeter, Templeton, 2017b; Dutour, Léna, & Lengagne, 2017b; Suzuki, Wheatcroft, & Griesser, 2016; Suzuki, Wheatcroft, & Griesser, 2017). A latency period of 10 min was systematically observed between playback of the associative learning stimulus and playback of mobbing calls in order to avoid carryover effects.

Statistical analysis

Analyses were done using SAS 9.4 (SAS Institute Inc., Cary, NC, U.S.A.) and R v.2.15.1 softwares (The R Foundation for Statistical Computing, Vienna, Austria, http://www.r-project.org). We first examined whether the begin call propensity varied between treatment groups during the nestling period. For this purpose, we analyzed the call propensity recorded each day before broadcasting the treatment using a logistic linear mixed model (LLMM) for which the call propensity was treated as a repeated dependent binary variable. To this aim, nest was considered as a random effect and the correlation between successive observations recorded on the same nest was specified using an autoregressive covariance structure. The treatment group, the time elapsed since hatch as well as their interactive effect, were introduced as fixed effects. The significance of each fixed effect was tested using a non-sequential F test and the Kenward-Roger method was used to approximate the denominator degree of freedom (SAS 9.4). Non-significant terms were successively dropped to obtain the final model. We used a similar model framework to compare the propensity of nestlings to stop begging after the onset of the broadcasting treatment according to the treatment group and the time elapsed since hatch. For this purpose, all observations for which nestlings were not calling before the onset of the playback treatment were discarded from the analysis. We used a Fisher exact test to test whether the begging calls propensity just after the playback of the associative learning stimulus only when nestlings were between 19 days post hatch and fledging day varied according to the group (associative learning or control). To study the nestling physiological response (i.e. corticosterone level) at baseline level when nestlings were 13 days old, we first performed a permutation test. Next, we used a Wilcoxon test to study the response after playback of associative learning stimulus (at 15 days old).

To investigate the behavioural responses of fledglings, we first examined whether the number of horizontal scans varied between treatment groups and the playback during the fledgling period. For this purpose, we ran generalized linear mixed models (GLMM) which included the treatment group, the playback (associative learning stimulus or mobbing calls) and their interactive effect as a fixed terms and nest as a random term. We used a negative binomial error distribution and log-link function for this analysis (*glmer.nb* in the package *lme4*; Bates et al. 2014). Secondly, to investigate the call propensity (N = 106), we used a binomial error distribution and logit-link function (*glmer* in the package *lme4*; Bates et al., 2014) (calling response = 1; no calling response = 0). As above, nests were introduced in the model as a random effect. The treatment group, the playback and their interactive effect were introduced as fixed effects. For both scanning and call propensity, we further conducted pairwise comparisons (*glht* in the package *multcomp*). Finally, because approaching and fleeing behaviours (two behaviours linked to movements) were opposed to immobility behaviour (see Appendix 3, Fig. A3), all approaching and fleeing individuals were regrouped within a unique category (hereafter moving individuals) and compared to the individuals who stayed still. To compare the propensity of fledglings to move *vs* individuals who stayed still according to the treatment group and the playback, we used a binomial error distribution and logit-link function. We then focused our analysis on moving individuals only (i.e. fleeing and approaching individuals; N = 23). Because only one of the control fledglings moved when exposed to the playback of associative learning stimulus, we discarded this group for our analyses (N = 22). Because only a small number of fledglings moved, Fisher exact tests were used to investigate the variation in mobbing propensity (i.e. approach) according to the treatment group and the playback.

Ethical note

Our study adhered to the ASAB/ABS Guidelines for the ethical treatment of animals. Our work was carried out under permission from the Prefecture du Rhône (Ref 2015-13) and with the approval of the ethic's committee at Lyon 1 University, France (permit number: 2017012410184917). Concerning ethical rules, all authors are accredited for performing experiments with living animals (French diploma "Experimentation animale" first level for researchers). All the manipulations were performed with great respect of animal welfare. After ringing, all nestlings were readily accepted back by their parents.

RESULTS

Behavioural and physiological responses of nestlings

The propensity to call before the playback treatment did not significantly vary according to the time elapsed since hatching but it was significantly higher for the associative learning group than the control one (*N* = 1420, treatment effect: $F_{1,341}$ = 4.17, *P* =0.042 ; time effect: $F_{1,426}$ = 0.66, *P* = 0.417; interaction: $F_{1,425}$ = 0.40, *P* = 0.529). The propensity to stop calling after the onset of the broadcasting treatment significantly increased according to the time elapsed since hatching but did not varied between treatment groups although call suppression tended to increase with time slightly more for the control group than for the associative learning one (*N* = 353, treatment effect: $F_{1,156}$ = 0.11, *P* = 0.745 ; time effect: $F_{1,176.}$= 46.19 , *P* < 0.0001; interaction: $F_{1,170}$ = 3.69, *P* = 0.057). We did not detect a treatment group effect on the nestling's response to the playback of the associative learning stimulus (*N* = 11, *P* = 0.608). Concerning physiological responses, corticosterone levels did not significantly differ between the treatment groups neither at 13 days old (i.e. baseline level) (*N* = 10, t = 0.6703; P = 0.639) nor at 15 days old, just after the playback of the associative learning stimulus (*N* = 10, W = 17; P = 0.4206; see Appendix 4, Fig. A4).

Behavioural responses of fledglings

Scanning response was significantly affected by the interaction between the stimuli that was broadcast (associative learning stimulus or mobbing calls) and the treatment group (associative learning and control) (Table 1; Fig. 1). In response to mobbing calls playback, the rate of horizontal scans did not differ between the two groups (*P* = 0.99; Fig. 1). It was higher during playback of mobbing calls than during the playback of the associative learning stimulus for the control group (*P* = 0.004; Fig. 1) while it did not differ for the associative learning group (*P* = 0.99; Fig. 1). Similar variations were found for the call propensity as indicated by a significant interaction effect between the group and the playback (Table 1; Fig. 2), although these variations were not statistically different between both groups in response to the associative learning stimulus playback (*P* = 0.95; proportion of calling: associative learning = 22.5%; control = 6.7%). Furthermore, there was a significant effect of playback on the probability of moving (i.e. approaching and fleeing behaviours), whereas group had no significant effect (Table1; Fig. 3). In response to mobbing calls, fledglings were more likely to move than in response to associative learning stimulus playback. Nonparametric tests indicate that (i) individuals from the control group were more prone to approach the loudspeaker than associative individuals in response to the mobbing call playbacks (*N* = 17; Fisher test: *P* = 0.049; see Fig. 3) (ii) approaching behaviour of individuals from the associative group did not differ between the two playbacks (*N* = 16; Fisher test: *P* = 0.999; see Fig. 3).

Table 1

Generalized linear mixed models (GLMM) results for the playback (associative learning stimulus or mobbing calls) and the group (associative learning or control) as predictors of variation in fledglings response behaviours. Significant P values are indicated in bold.

Behaviours	GLMM			
	Explanatory variables	df	χ^2	*P*
scanning	playback	1	5.8243	**0.0158**
	group	1	6.1785	**0.0129**
	playback *group	1	5.4487	**0.0196**
calling	playback	1	0.9227	0.3368
	group	1	0.0247	0.8752
	playback *group	1	4.8979	**0.0269**
approaching + fleeing	playback	1	8.9545	**0.0028**
	group	1	1.6161	0.2036
	playback *group	1	0.8797	0.3483

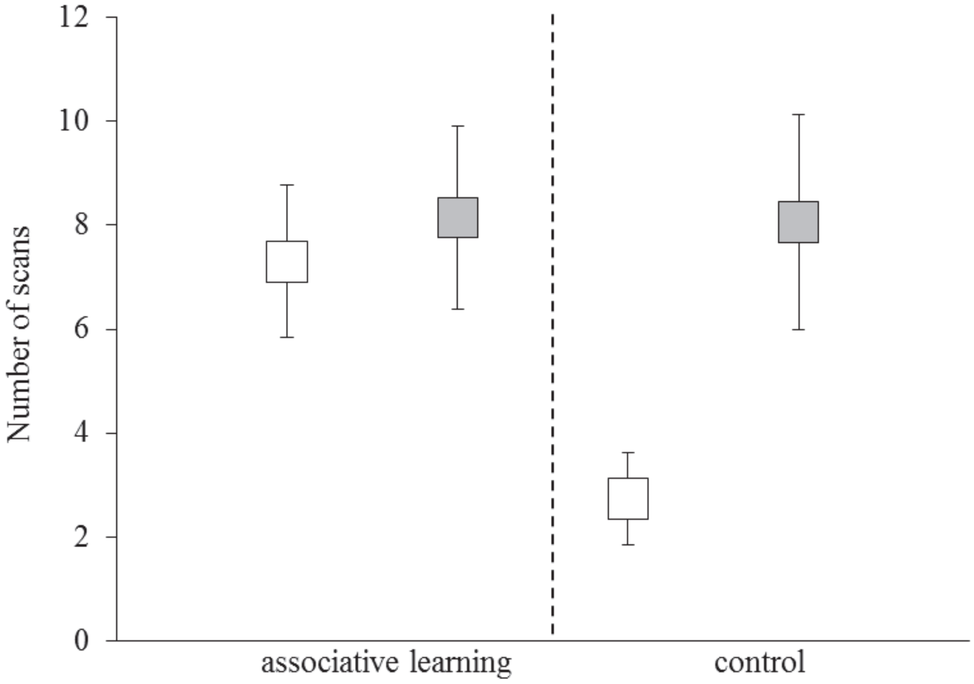

Figure 1. Number of horizontal scans made by associative learning and control fledglings during the playbacks of associative learning signal (white) and mobbing calls (grey) (mean ± SE).

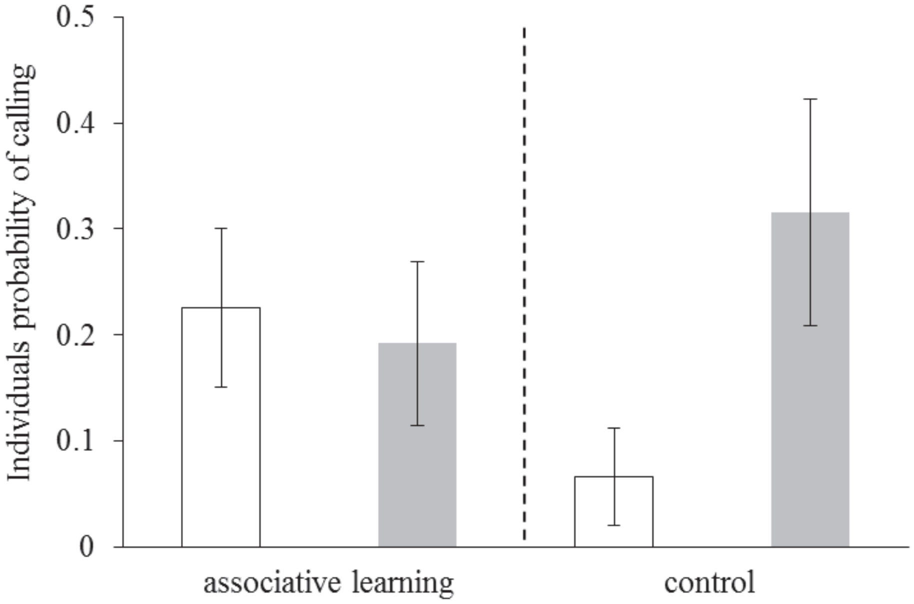

Figure 2. Associative learning and control fledglings probability of calling during the playbacks of associative learning signal (white) and mobbing calls (grey).

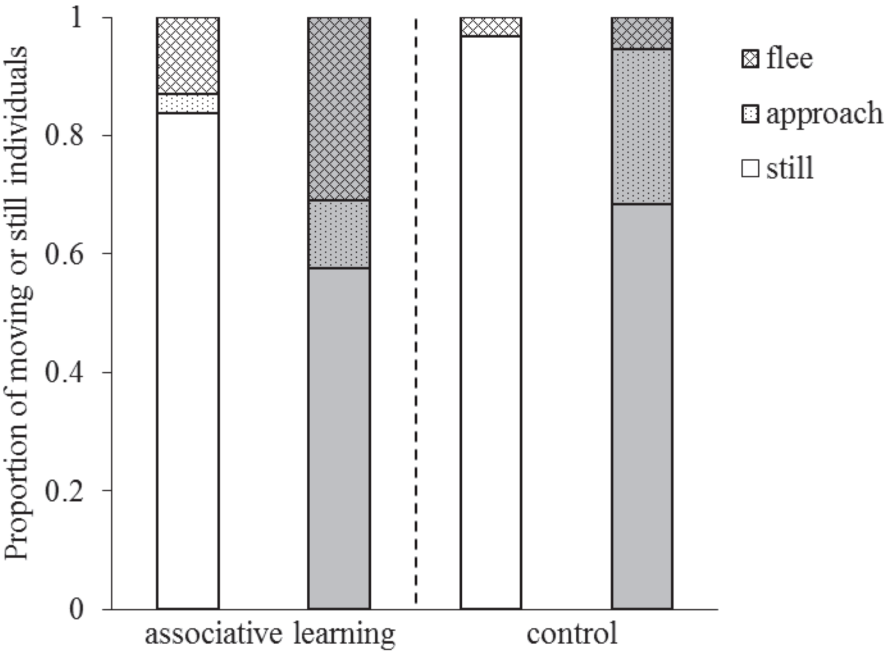

Figure 3. Response of fledglings to the playbacks of associative learning signal (white) and mobbing calls (grey).

DISCUSSION

Here, we investigated whether listening to a novel stimulus associated with mobbing calls during the nestling period made nestlings recognize this stimulus as an indicator of threat proximity when fledglings. We experimentally showed that fledglings learn to associative previously novel stimuli with mobbing calls and exhibit vigilance behaviours in response to the novel stimuli whereas they are unable to do so during the nestling phase.

Effect of the associative learning treatment during the nestling phase

Several studies have shown that nestlings become silent when they hear playbacks of their parents' alarm calls (Barati & McDonald, 2017; Davies, Madden, & Butchart, 2004; Haff & Magrath, 2012; Madden, Kilner, & Davies, 2005; Platzen & Magrath, 2004). However, most of these studies have opposed alarm calls with background noise or sympatric species stimuli (i.e. stimuli known). In the present study, nestlings suppressed calling to associative learning stimulus equally to the mobbing call playbacks, suggesting that novelty (i.e. a stimulus never heard before) alone may be used as a signal of danger (Curio, Ernst, & Vieth, 1978b; Schaller & Emlen, 1961). We found that, contrary to young nestlings, older ones strongly reduced begging calls in response to the associative learning stimulus and mobbing calls, suggesting that older nestlings are less prone to recognition errors than younger ones (Davies & Brooke, 1988; Davies, Madden, & Butchart, 2004). This pattern of gradual acquisition is in accordance with previous studies conducted on nestling great tits (Rydén, 1978). We did not detect a group effect on the nestling's response to the playback of the associative learning stimulus at the end of the learning period but the low sample size may have reduced our ability to detect a significant pattern. A detailed study of nestling behaviours and physiology would also be insightful to actually address this question.

Although many nestlings respond to mobbing calls with anti-predator behaviour, the physiological responses to such calls are poorly understood. In this study we found no evidence of an adrenocortical response in great tit nestlings, even though they were at a developmental stage in which Hypothalamo-Pituitary-Adrenal (HPA) axis reactivity leads to measurable corticosterone secretion (Stöwe et al., 2010). Contrary to our predictions, at 15 days post hatch, associative learning nestlings that were exposed to mobbing calls did not exhibit higher corticosterone levels than control nestlings that were not exposed to mobbing calls. This suggests that they did not associate the novel acoustic stimulus with mobbing calls from a physiological point of view. This result is in accordance with others studies conducted on nestling bird species such as white crowned sparrow, *Zonotrichia leucophrys*, and American kestrel, *Falco sparverius*, (Dufty & Crandall, 2005; Rivers et al., 2011). Several non-exclusive explanations can explain our results. Mobbing calls could stimulate increased secretion of corticosterone to mobilize energy reserves in anticipation of an interaction with a predator. We measure corticosterone level when nestlings were 13 and 15 days old when they are exclusively in the nest. Our results may be linked to the fact that these young nestlings may not be physically capable to take evasive action. In addition, elevated corticosterone levels are known to be costly in term of growth and development (Wada & Breuner 2008; Rivers et al., 2011) and such corticosterone level may outweigh the benefice of the response (Dufty & Crandall, 2005). Studies with additional species and other stages of nestling development should be investigated to assess the generality of this finding. At least, because corticosterone responses can vary markedly between birds sampled under the same conditions (Cockrem & Silverin, 2002) (i.e. in a nest some nestlings are shy whereas others are bold; Schwabl, 1995; Verbeek, Drent, & Wiepkema, 1994), we cannot exclude that pooling 10 nestlings of the same nest could mask individual differences in response.

Mobbing calls recognition and associative learning in fledglings

Fledglings exhibited a higher rate of scanning when hearing the associative learning stimuli but only if it was associated with mobbing calls during the nestling phase. A similar trend was also observed concerning the calling activity as well as the proneness to move. Altogether, these results indicate that individuals associated the artificial sound with conspecific mobbing calls without having to see the mobbing scene. Scanning rate is a good proxy of vigilance effort (Creel, Schuette, & Christianson, 2014; Huang, Sieving, & St Mary, 2012; Lendrem, 1983) suggesting that animals actually perceived the associative learning stimulus as an indicator of threat proximity only if it was associated with mobbing call during the learning phase. Whether fledglings associated the artificial stimulus as the source of threat itself or as heterospecific mobbing calls (indicating the presence of a threat) and whether the whole ontogeny of mobbing behaviour relies only on learning process, remain both open questions. Correlations between the rate of response development and the magnitude of exposure to heterospecific alarm calls provide evidence for learning. For instance, infant vervet monkeys, *Cercopithecus aethiops pygerythrus*, develop responses to superb starling, *Lamprotornis superbus*, mobbing calls more quickly on territories where these birds are common, suggesting that those young have more opportunities to learn about the calls than young on territories where starlings are less common (Hauser, 1988; Magrath et al., 2015b). Concerning adults, Magrath et al. (2015a) showed that superb fairy-wren, *Malurus cyaneus*, can associate novel sounds with visual stimuli of a known predator. One may thus expect that learning process, association of a known threat with the conspecific mobbing call, can operate in the wild. Such mechanisms could make the set of recognized heterospecific mobbing calls adjusted to the local composition of prey communities, which is also congruent with field studies reporting local variations of the rate of responses towards heterospecific mobbing calls (Wheatcroft & Price, 2013).

In addition to such associative learning processes, our study also reveals that fledglings responded to conspecific mobbing calls despite the learning treatment they experienced. Indeed, in both groups, hearing conspecific mobbing calls resulted in increased vigilance, a higher proneness to call as well as movement. Since all these tests were performed on the fledging day, we can safely assume that all animals could not have had the opportunity to observe a mobbing scene before the tests. Our results therefore indicate that juveniles do not need to observe mobbing events to respond to mobbing calls. Although juvenile great tits do not respond to mobbing calls by exhibiting a complete, adult like mobbing behaviour, they do produce some of the mobbing behaviours performed by adults. Two hypotheses, not mutually exclusive, could be suggested to explain responses to mobbing calls: the response (1) is at least partly innate or (2) is due to the impregnation on the basis of acoustic stimuli heard during nestling phase. Mobbing calls are composed of ABC notes which are involved in vigilance and D notes involved in foraging flocks or to recruit partners during the breeding season and receivers respond by approaching the caller (Japanese great tit, *Parus minor*: Suzuki, Wheatcroft, & Griesser, 2016; great tit: Dutour, pers. observation). In the present study, tests were performed during the fledgling when great tits form family groups and often use D notes on their own to maintain group cohesion (Dutour, pers. observation). The responses of fledglings could be related to the context (i.e. presence of family members in the vicinity), or could be due to the sensitivity to the D notes. Furthermore, contrarily to fledglings belonging to the control learning group, those belonging to the mobbing learning group were more prone to flee than approach the loudspeaker. This suggests that reinforcement with mobbing calls during the nestling phase altered mobbing learning. Such impairment could be either due to call overexposure, as previously shown in vocalization learning (Brainard & Doupe, 2013; Tchernichovski et al., 1999), or because of the absence of a threat associated with the mobbing call during exposure.

Conclusion

This study suggested that nestling great tits can't discriminate between two different acoustic signals but demonstrated that they associate mobbing calls with a previously novel sound when they were outside the nest cavity. Nevertheless, the fledglings did not respond with typical mobbing behaviour (i.e. approach and harass), and thus for the development of these specific responses likely require experience of parental visual response (i.e. cultural transmission) (Kullberg & Lind, 2002). The present findings raise questions about how nestlings extract information about the nature of predators and how finely they can discriminate between different acoustic stimuli.

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Discussion générale

Les objectifs de cette thèse sont de comprendre comment une réponse au prédateur se met en place et les règles de la communication intraspécifique et interspécifique dans le cas du comportement de harcèlement chez les passereaux (36 espèces). Alors que jusqu'à présent l'essentiel des travaux de recherche traitant de la communication concernaient les échanges d'informations au sein d'une même espèce, mon travail a mis en évidence un partage d'informations entre espèces différentes pour faire face au prédateur. En utilisant une approche multidisciplinaire impliquant la bioacoustique, la biologie comportementale, l'écologie, la physiologie et en utilisant différentes échelles allant de la communauté à l'individu, j'ai identifié les mécanismes susceptibles d'expliquer cette stratégie dans sa globalité.

I/ Le harcèlement du prédateur : une stratégie efficace

1) Principaux facteurs déterminants la mise en place du harcèlement

La sélection exercée par la prédation est à l'origine de l'apparition de stratégies anti-prédatrices permettant aux proies d'augmenter leur chance d'échapper à la prédation (Lima & Dill 1990). Le harcèlement du prédateur est une stratégie anti-prédatrice particulière faisant fuir le prédateur et on s'attend donc à ce qu'elle dépende du risque de prédation. J'ai montré que le harcèlement est **spécifique à l'espèce prédatrice** : la chevêchette suscite l'intérêt des passereaux, puisque très vite après l'émission de son cri une multitude d'espèces tourne autour du haut-parleur, alors qu'ils sont indifférents à la chouette non prédatrice (la tengmalm) (Article 1), validant ainsi la *mobbing plasticity hypothesis*, qui prédit que les oiseaux peuvent reconnaître le risque posé par les prédateurs (Caro 2005) et ajuster leur comportement de harcèlement en conséquence (Cunha et al. 2017). Généralement, les proies harcèlent les prédateurs et ne harcèlent pas les espèces non prédatrices. Pourtant, dans certains cas, des individus harcèlent des animaux ne posant pas de menace. C'est le cas par exemple de certaines espèces qui vivent en groupe comme le sapajou capucin (*Cebus capucinus*) ou le suricate (*Suricata suricatta*) (Graw & Manser 2007, Perry & Manson 2008) pour lesquelles le harcèlement d'une espèce qui n'est pas menaçante représenterait une occasion de s'exercer au harcèlement sans prendre de risque de se faire capturer par le prédateur. Ce comportement pourrait également être important pour renforcer les relations sociales.

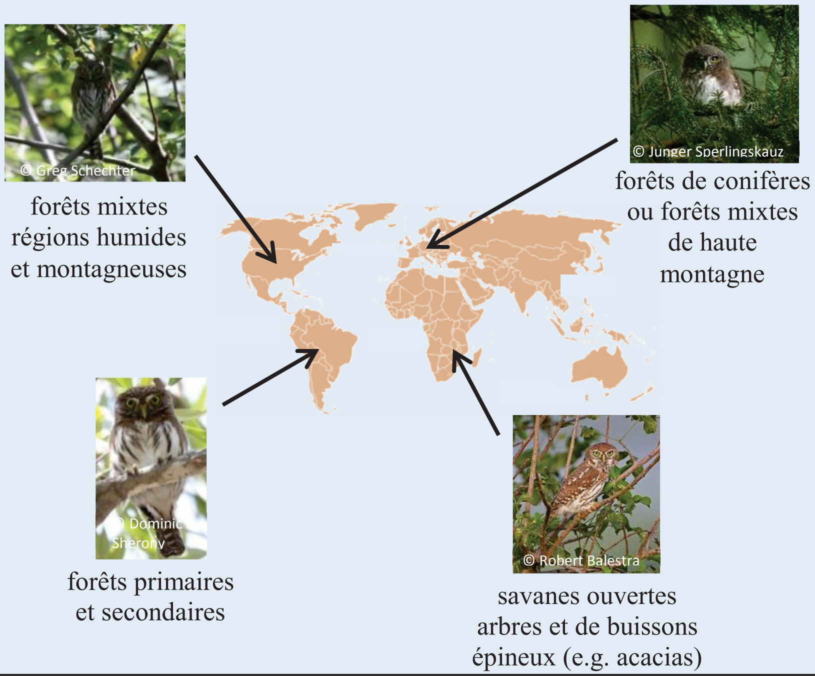
Toutes les espèces qui harcèlent font partie du **régime alimentaire du prédateur** et les espèces qui répondent le plus au prédateur sont celles qui subissent la **plus forte prédation** (**Article 2**). La mésange noire par exemple subit une forte prédation (Suhonen et al. 1993, Chassagnard et al. 2008) et est présente dans 80% des cas de harcèlement lors de la repasse chevêchette. Les prédateurs attaquant rarement des proies plus grosses qu'eux chez les oiseaux (lien mécanique avec le vol) (Valcu et al. 2014), seules les espèces qui se situent dans la fourchette de taille des proies potentielles devraient s'engager dans le harcèlement du prédateur. Ainsi, il a été montré chez les oiseaux tropicaux que les espèces qui harcèlent sont plus légères que les espèces qui ne harcèlent pas et sont toutes **plus petites que le prédateur harcelé** (Cuhna et al. 2017). Nos résultats confirment ce pattern : les espèces plus grosses que la chevêchette (50-80g) comme le merle noir (*Turdus merula*) (80-110 g) ou le geai des chênes (*Garrulus glandarius*) (140-190g) ne harcèlent pas car elles ne sont pas prédatées (**Article 2**) alors que les **petites espèces, sensibles à la prédation**, mettent en place la stratégie du harcèlement. Ce ratio de taille prédateur/proie est également retrouvé chez les mammifères excepté chez des grandes espèces terrestres et aquatiques comme l'éléphant d'Afrique (*Loxodonta africana*) (McComb et al. 2011) et la baleine à bosse (*Megaptera novaeangliae*) (Pitman et al. 2017). Plus la pression de prédation augmente et plus il y a de chance que le comportement de harcèlement se mette en place. Plusieurs études suggèrent d'ailleurs une corrélation positive entre la pression de prédation locale et la force de réponse de harcèlement chez les oiseaux (Krams et al. 2010, Sandoval & Wilson 2012, Tilgar & Moks 2015). Dans mes deux zones d'études (Monts du Lyonnais et Bugey), malgré une composition de prédateurs différente, la réponse au harcèlement fonctionne très bien (Article 1).

Nos résultats indiquent un patron saisonnier dans la réaction des passereaux à la présence de la chouette chevêchette avec une **propension à harceler plus élevée en automne** (**Article 2**). Le cas de la chevêchette est ainsi unique en son genre puisque dans la littérature une tendance accrue au harcèlement est notée au printemps pendant la saison de reproduction (Altmann 1956, Shedd 1982, Zimmermann & Curio 1988, Swaisgood et al. 1999, Nijman 2004, Krams et al. 2009). Toutefois, la plupart de ces études ont été menées vers les nids augmentant « artificiellement » les réponses des adultes au printemps ou n'ont pas contrôlé les variations de communautés de proies entre les saisons. Dans notre étude, la sensibilité particulière des passereaux au cours de la saison peut s'expliquer par une modification du régime alimentaire des rapaces. Dans les forêts boréales de conifères, la chevêchette s'est révélée être le principal prédateur des passereaux durant l'hiver (Mikkola 1983, Solheim

1984), ce qui était probablement le cas dans notre zone d'étude (Y. Muller, communication personnelle). Dès que les conditions météorologiques deviennent défavorables (neige au sol) et réduisent la possibilité de capturer des rongeurs l'alimentation de la chouette chevêchette se compose alors en grande partie d'oiseaux. Cette modification du régime alimentaire au cours de l'année correspond parfaitement avec le pattern de réponse des passereaux que j'ai mis en évidence dans notre étude avec une augmentation importante du harcèlement chez les espèces fortement consommées par la chouette en automne.

Les études menées jusqu'à présent indiquent que le comportement de harcèlement est fréquemment observé envers les rapaces du **genre *Glaucidium*** et se retrouve sur tous les continents où ils sont présents. Par exemple, dans le sud du Brésil, la chevêchette brune (*Glaucidium brasilianum*) est souvent assaillie par un cortège d'espèces aviaires (Motta-Junior 2007, Reudink et al. 2007, Sandoval & Wilson 2012, Tilgar & Moks 2015, Cunha et al. 2017) tout comme la chevêchette naine (*Glaucidium gnoma*) aux États-Unis (Deppe & al. 2003, Templeton et al. 2005, Templeton & Greene 2007, Nocera & Ratcliffe 2009) ou encore la chevêchette perlée (*Glaucidium perlatum*) en Afrique du sud (Engesser et al. 2016) (encadré 1). Il reste à déterminer si ce type de comportement est observé chez la trentaine d'espèces du genre *Glaucidium*. Le cas échéant, une analyse comparative prenant en compte le type de milieu et la communauté de proies permettrait de comprendre une grande partie des mécanismes impliqués dans la réponse au prédateur.

Encadré 1: Distribution géographiques des différentes espèces de chevêchette harcelées et vivants dans des milieux différents



Le harcèlement du prédateur ne se limitant pas au genre *Glaucidium*, que se passe-t-il dans le cas des autres rapaces mangeurs d'oiseaux comme le faucon pèlerin (*Falco peregrinus*), l'épervier d'Europe (*Accipiter nisus*) ou encore le pygargue à queue blanche (*Haliaeetus albicilla*) ? Dû à son immense territoire de chasse et rayon d'action, le faucon pèlerin ne semble pas être un bon candidat pour le harcèlement du prédateur. Contrairement au faucon pèlerin, l'épervier a un territoire de chasse plus petit et suscite le harcèlement lorsqu'il est visible généralement en vol. L'épervier ne se fait pas harceler quand il est posé car il ne chante pas et ne donne pas sa position contrairement à la chevêchette qui, lorsqu'elle chante, **donne sa position** exacte et attire une foule de passereaux « surexcités ». Les observations faites par Thierry Lengagne dans le Haut-Bugey (Ain) confirment cette idée puisqu'il a déjà observé une chevêchette silencieuse très bien visible (posée sur une branche de conifère dépourvue d'épine) ne suscitant pas le harcèlement. Lors des repasses de chevêchettes (**Articles 1 et 2**), j'ai également eu l'occasion d'observer une chevêchette silencieuse située dans l'arbre juste au-dessus du haut-parleur qui mimait sa présence. Celle-ci ne suscitait pas l'intérêt des passereaux contrairement à la repasse. A contrario, sur plusieurs sites, l'arrivée de la chevêchette pendant la repasse nous a causé quelques problèmes car tous les oiseaux se dirigeaient vers elle lorsqu'elle se posait dans un arbre et chantait. Si la **détection** de cette petite chouette de moins de 20 cm semble difficile lorsqu'elle ne chante pas, que se passe-t-il lorsque le prédateur est très grand ? La taille imposante du pygargue (environ 80 cm de hauteur) ne joue pas en sa faveur. En effet, ce gros rapace est souvent harcelé par les corneilles qui le détectent facilement lorsqu'il est posé à terre ou dans un arbre.

Le comportement de harcèlement devrait se mettre en place face à des espèces de **prédateurs solitaires et isolés** puisque dans le cas des espèces de prédateurs vivant en groupe le risque de se faire capturer par un autre membre du groupe est non négligeable. Alors que 5 espèce de primates évitent de s'approcher du chimpanzé (*Pan troglodytes*) (Zuberbühler et al. 1999), connu pour vivre et chasser en groupe (Boesch & Boesch 1989), une autre espèce de primate, le colobe bai (*Procolobus badius*), peut le harceler et s'engager parfois jusqu'au combat mais cette stratégie s'avère généralement inefficace pour dissuader le prédateur (Stanford 1996, Mitani & Watts 1999). Dans les cas où le harcèlement se met en place contre un prédateur appartenant à un groupe, les proies harcèlent seulement si leur nombre est au minimum trois fois plus élevé par rapport aux prédateurs (e.g. Trinkel & Kastberger 2005) ou si la taille des proies est beaucoup plus grande que celle des prédateurs (McComb et al. 2011, Pitman et al. 2017).

Le **mode de vie du prédateur** (nocturne ou diurne) pourrait également influencer la réponse au harcèlement. En effet, dans le cas où le risque de prédation ne diffère pas entre les deux types d'espèces prédatrices, les prédateurs diurnes constituent une menace la journée et par conséquent, le risque associé au harcèlement (i.e. se faire capturer) est plus élevée chez un prédateur diurne que nocturne qui ne constitue pas un danger immédiat (Cunha et al. 2017). Ainsi, il est peut-être moins coûteux d'harceler un prédateur nocturne qu'un prédateur diurne en journée puisque que le risque de se faire capturer est très faible. Mes résultats indiquent cependant le contraire (**Article 1**) mais ils peuvent s'expliquer par le faible risque de prédation posé par l'espèce nocturne. En réponse aux deux espèces de chouettes nocturne et diurne, je ne sais pas quelle est la part liée à la vision ou au son. Mes résultats montrent que les oiseaux font très bien la différence entre des signaux acoustiques de chevêchette et de tengmalm mais feraient-ils la différence entre ces deux types de chouettes si elles étaient empaillées ? Je pense que si on plaçait une chouette de tengmalm en haut d'un arbre en évidence dans un territoire à chevêchette les oiseaux viendraient harceler même si il a été montré que l'intensité du harcèlement est influencé par la présence ou l'absence des taches blanches situées derrière la tête des chevêchettes (Deppe et al. 2003).

Face à des prédateurs pour lesquels la stratégie de harcèlement n'est pas efficace et se révèle trop coûteuse, les proies peuvent développer une **stratégie alternative** comme l'émission d'une multitude de cris pour faire partir le prédateur car celui-ci a compris qu'il était détecté (e.g. Zuberbühler et al. 1999). Dans ce cas les individus s'approchent un peu mais ne harcèlent pas, ne prenant aucun risque de se faire capturer par le prédateur. Cette stratégie ne permet pas de faire partir le prédateur autant que la stratégie du harcèlement mais permet de diminuer le coût principal du harcèlement, la capture et la mort de la proie. Si le prédateur représente un danger immédiat, les proies fuient et émettent des signaux d'alarme envers leurs congénères. Dans ce cas de l'alarme, la structure du signal émis rend l'émetteur difficilement localisable par le prédateur (Marler 1955, Ficken & Popp 1996).

2) Processus coévolutifs résultant d'interactions entre proies et prédateurs : la course aux armements est-elle lancée ?

La détection, et donc le harcèlement de la chevêchette par les passereaux, est liée à son signal acoustique. Pourquoi la chouette utilise-t-elle ce signal acoustique qui lui impose le coût du harcèlement ? Pour cette espèce vivant en milieu forestier, le chant est essentiel pour les interactions sociales et donc la défense de son territoire. Face au harcèlement mis en place par les proies, la chevêchette pourrait utiliser ce système, en tirer bénéfice et dans ce cas, la stratégie de harcèlement se retournerait comme un piège sur les passereaux. Plusieurs observations naturalistes indiquent que pendant la saison de reproduction, lorsque le mâle chante et se fait harceler par les passereaux, la femelle qui n'est pas loin profite de la situation et du moment idéal pour capturer un oiseau occupé à harceler. Cette stratégie mise en place par le prédateur est, à ma connaissance, méconnue chez les autres espèces de prédateurs. Cela mériterait d'être quantifié même si cette tâche est probablement difficile compte tenu des heures de prospections et d'observations que cela demande.

3) Que faire face à un prédateur inconnu ?

a) Pas de harcèlement face à un prédateur inconnu

Au cours de mon travail, en mimant la présence de chouette chevêchette à l'aide d'un haut-parleur dans des zones avec ou sans chevêchette, j'ai montré qu'une réponse des passereaux est observée lorsque les tests sont effectués dans les territoires occupés par une chouette. En revanche, aucune réponse des oiseaux n'est notée lorsque celle-ci est absente (Article 1). Il s'agit donc d'un **ajustement comportemental anti-prédateur local**, se mettant en place uniquement dans l'environnement où le **prédateur est présent**. La pression de prédation joue donc un rôle primordial dans l'apparition du comportement de harcèlement. La réponse au prédateur dans la zone où il est présent est liée soit à un processus de sélection (adaptation locale) soit à un phénomène d'apprentissage où les démonstrateurs sont essentiels (Francis et al. 1989, Graw & Manser 2007). Mes analyses ne me permettent pas de conclure quant au caractère inné ou acquis du comportement de harcèlement. Pour ségréger ces deux possibilités, il faudrait faire des transferts de ponte de passereaux entre les deux zones et voir si les oisillons provenant de la zone où la chevêchette est présente harcèlent le prédateur lorsqu'ils sont élevés dans la zone où la chevêchette est absente. Dans l'affirmative, alors je pourrais conclure qu'une adaptation locale façonne la mise en place du comportement de harcèlement. Ainsi, il serait très avantageux pour un prédateur d'arriver dans une zone où il n'est pas connu puisqu'il ne serait pas chassé de cette zone dès sa détection. Dans ce cas il serait possible d'étudier combien de temps les proies mettent pour développer cette stratégie puisqu'un processus d'apprentissage efficace introduit nécessairement un délai entre le moment où les récepteurs réagissent pour la première fois aux signaux de façon provisoire et lorsqu'ils y répondent fortement (Shriner 1999). Les deux sessions de prospections faites en octobre 2015 et janvier/février 2016 dans le Haut-Bugey indiquent que ce comportement de harcèlement face à la chouette chevêchette est très plastique. En effet, lors de la première session au moment du chant d'automne sur un site où la chouette était présente les passereaux ont répondu à la repasse de chevêchette. Quelques mois plus tard lors de la deuxième session de prospection la chevêchette n'était plus sur le site et le harcèlement des passereaux avait disparu. Ces observations indiquent qu'il suffit de 4-5 mois pour que la réponse au prédateur disparaisse et suggèrent donc une part importante liée à l'apprentissage. On peut imaginer la même chose pour l'apparition du comportement, même si je pense que ce processus d'apprentissage est un peu plus long.

b) L'ontogenèse du comportement de harcèlement et son rôle dans la reconnaissance des prédateurs

Les jeunes semblent avoir besoin d'un certain degré d'expérience avec les nouveaux prédateurs pour les reconnaître comme des menaces (Graw & Manser 2007). Chez les espèces vivant en groupe comme le geai à gorge blanche (*Aphelocoma coerulescens*) ou le suricate, les jeunes apprennent à harceler les prédateurs en observant les adultes (Francis et al. 1989, Graw & Manser 2007). Le comportement de harcèlement de chaque individu change avec l'expérience et chaque individu façonne son comportement de façon à optimiser sa stratégie. Face à des signaux de harcèlement, les jeunes mésanges charbonnières exhibent la séquence complète du comportement de réponse au harcèlement (scanne, émission de cris et approche du haut-parleur) mais cette séquence peut être perturbée si les jeunes ont été exposés quotidiennement aux cris de harcèlement (voir partie II.1) (**Article 7**). Bien que le comportement de harcèlement soit bien étudié chez un certain nombre d'espèces (Altmann 1956, Crofoot 2012, Gill & Bierema 2013) et que le développement de la reconnaissance des prédateurs suscite beaucoup d'intérêt (Curio 1993, Kelley & Magurran 2003, Griffin 2004, Hollén & Radford 2009), à ma connaissance il n'y a pas d'étude concernant l'ontogénie du comportement de harcèlement, depuis la première réponse d'un individu jusqu'à son comportement de harcèlement au stade adulte. L'étude du développement du comportement de harcèlement et de la reconnaissance des prédateurs permettrait de mieux comprendre les réactions au cours de la vie d'un individu. Les étapes ontogénétiques de ce comportement pourraient être étudiées en manipulant le moment où les individus sont confrontés pour la première fois à un évènement de harcèlement. Cela nécessite de se substituer au tuteur (parent) et mener des expériences en volière. Ces travaux permettraient de déterminer s'il existe une phase sensible pour le développement de ce comportement. En comprenant la manière dont le harcèlement est acquis et évolue avec le temps, on pourrait tester les manières dont la pression de prédation locale peut influencer les comportements de harcèlement à échelle de la population. Cela fournirait également des informations sur la flexibilité des jeunes et des adultes dans leur apprentissage au harcèlement. On peut également se demander si les meilleurs harceleurs (i.e. ceux qui détectent vite le prédateur et harcèlent le plus) sont les individus les plus vieux avec le plus d'expérience. La réponse à toutes ces questions nécessite un suivi individuel passant par une approche expérimentale permettant de manipuler le contenu de l'information.

4) Comment l'habitat façonne le comportement de harcèlement

La réflexion qui suit part d'un constat : lors de ma collecte de cris de harcèlement pour étudier les forces évolutives exercées sur les signaux, sur 23 espèces étudiées, une seule vivait dans un milieu ouvert (**Article 5**). Ainsi, le risque de prédation et donc la mise en place du comportement de harcèlement semble varier selon **les strates et les différents types d'habitats**.

La *safe niche hypothesis* prédit que les espèces vivant au sol devraient être moins susceptibles d'harceler un prédateur perché que les espèces vivant plus haut dans la strate comme la canopée (Cunha et al. 2017). Les espèces vivant au sol sont plus vulnérables aux prédateurs perchés et ayant une stratégie de chasse descendante (Ekman 1986, Suhonen 1993), car elles sont plus facilement tuées par ces prédateurs et ont moins de possibilités de s'échapper en cas d'attaque. A contrario, le harcèlement peut être une stratégie plus avantageuse pour les espèces vivant dans les arbres qui peuvent se cacher ou s'échapper plus facilement (Crofoot 2012). Les espèces vivant au sol développent généralement des stratégies alternatives pour faire face aux prédateurs perchés comme par exemple les Tinamidae et Caprimulgidae qui mettent en place la stratégie du camouflage.

Lorsqu'ils vivent en milieux ouverts, les oiseaux peuvent vivre isolés les uns des autres ou en groupe. Ce mode de vie impacterait le comportement de harcèlement. D'une part, les espèces solitaires qui vivent au sol harcèleraient les prédateurs terrestres uniquement (e.g. serpents) lorsqu'ils sont trop proches de leur nid (Ellison & Ribic 2012). D'autre part, le comportement de harcèlement des individus vivant en groupes sociaux stables comme le cratéope bicolore (*Turdoides bicolor*) (Engesser et al. 2016) et le geai à gorge blanche

(Francis et al. 1989) ou en colonies comme la sterne arctique (*Sterna paradisaea*) (Clode et al. 2000) ne se limiterait pas aux prédateurs terrestres. Dans ces différentes situations, le harcèlement du prédateur qui pourrait devenir un danger pour la progéniture est généralement lié à de la défense de nid ou du site occupé par les jeunes.

La **qualité du milieu** influence également la réponse au harcèlement qui est plus intense dans les forêts non aménagées que dans les jeunes forêts aménagées (Krama et al. 2012). Les différences de qualité du milieu sont susceptibles d'avoir des conséquences sur la survie des oiseaux. En effet, les oiseaux qui harcèlent le prédateur ont tendance à être visibles, courent des risques importants (Curio & Regelmann 1985, Ficken & Popp 1996) et devraient adapter leur comportement pour minimiser ces risques (Curio & Regelmann 1985, Ficken & Popp 1996, McLean & Rhodes 1991, Pavey & Smyth 1998).

A échelle plus large, le type d'habitat (insulaire ou continental) pourrait impacter le comportement de harcèlement mais cette hypothèse n'a, à ma connaissance, jamais été testée. En effet, il semble que le nombre d'espèces qui harcèlent et le comportement de harcèlement des espèces vivant en milieu insulaire comme le Japon ou l'Australie est plus important par rapport aux espèces continentales. Cette différence de réponse comportementale pourrait s'expliquer par un nombre plus important de prédateurs introduits et des densités de prédateurs élevées dans les milieux insulaires.

Le milieu dans lequel se trouve le prédateur peut également influencer son harcèlement. Les prédateurs peuvent se poser dans des milieux ouverts et fermés mais ils sont plus fréquemment chassés dans des habitats ouverts lorsqu'ils sont à découvert pendant la journée car plus visibles. Par exemple, les rapaces posés sur un piquet en pleine journée augmenteront leur probabilité d'être détectés et harcelés (e.g. Sieder et al. 2018).

5) Implications en biologie de la conservation

La détermination de l'aire de distribution des espèces et la taille des populations sont des éléments clés en termes de biologie de conservation. Chez les oiseaux, l'acquisition de cette connaissance passe souvent par l'utilisation des indices acoustiques que les animaux utilisent lors de la défense du territoire. Il est alors possible d'effectuer des écoutes passives en écoutant les chants émis spontanément ou de travailler avec un haut-parleur mimant l'arrivée d'un compétiteur de la même espèce afin de provoquer une réponse de l'espèce recherchée. Ce dernier cas est souvent utilisé pour travailler sur les rapaces comme la chevêchette d'Europe. Toutefois, les résultats obtenus dépendent de la probabilité de réponse de la chouette qui est très variable d'un mois à l'autre. Sur des sites où la chevêchette était présente, nos données de prospection tenant compte de la réponse de la chouette datant de juin 2015 indiquaient 100% de faux négatifs (n = 20) alors que celles de juillet indiquaient 17% (n = 12). Plutôt que de prendre en compte la réponse de la chouette elle-même, le travail que j'ai réalisé permet de valider la prise en compte de la réponse des passereaux lors de la **prospection de la chevêchette** puisque leurs comportements de harcèlement représentent un excellent indicateur de la présence de la chouette sur le site (Article 1) (Figure 7). Cette réaction des oiseaux face à un rapace est très bien connue des naturalistes (chevêchette : Géroudet 1965, Y. Muller, com. pers : pygargue : R. Probst & T. Lengagne com. pers.) mais n'avait à ma connaissance jamais été validée avec un protocole scientifique et une analyse statistique auparavant.

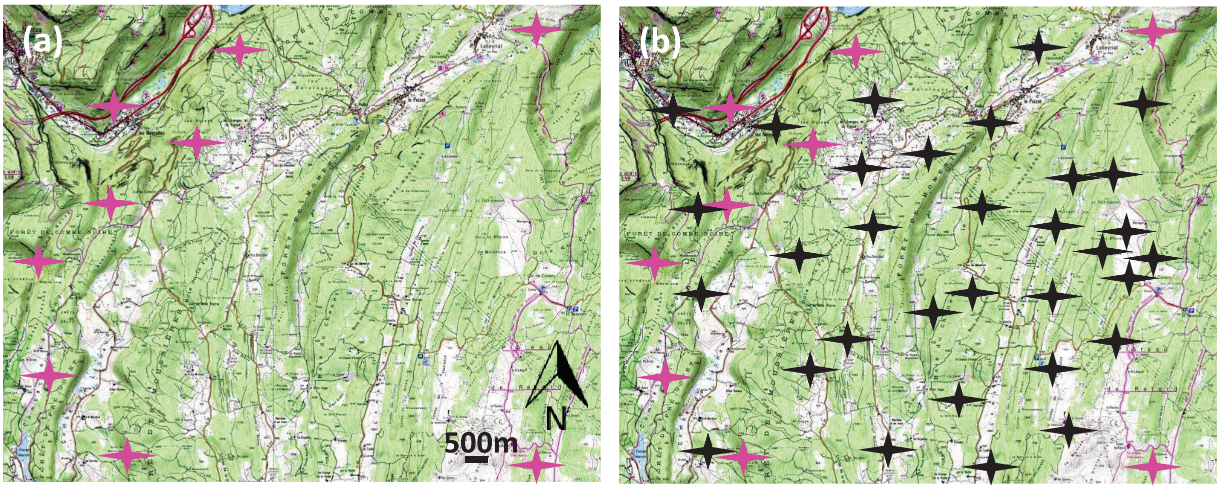


Figure 7 : Carte de prospection à la chevêchette d'Europe (Haut-Bugey, Ain): (a) nombre d'individus connus avant l'utilisation de la méthode tenant compte de la réponse des passereaux (croix roses) et (b) sites où la présence de la chouette est confirmée après l'utilisation de la méthode (croix noires).

La réponse aux repasses de cris de harcèlement est d'ailleurs une **méthode permettant d'estimer l'abondance des espèces** d'oiseaux en Amérique du Nord. Les repasses augmentent considérablement la probabilité de détection et d'observations visuelles des oiseaux par rapport aux observations silencieuses effectuées avant la diffusion des cris (Gunn et al. 2000, Turcotte & Desrochers 2002). J'ai également rencontré ce problème de détection lors des repasses du prédateur (Article 2). En effet, j'ai pu noter 25 fausses absences (i.e. une espèce a répondu à la repasse et n'a pas été détectée durant l'Indice Ponctuel d'Abondance (Blondel et al. 1970)).

Finalement, l'intensité du harcèlement peut être également prise en compte comme indicateur de **qualité du milieu**. En effet, le harcèlement est plus intense dans les forêts non aménagées où les oiseaux se reproduisent dans des communautés plus denses et plus diversifiées que dans les jeunes forêts aménagées (Krama et al. 2012).

Ainsi, la réponse au prédateur et aux cris de harcèlement se révèlent être des méthodes efficaces pouvant être utilisées en biologie de la conservation.

En conclusion, le comportement de harcèlement fonctionne pour certains types de prédateurs et dans certaines situations. Les proies mettent en place le harcèlement lorsque le risque de se faire capturer par le prédateur est faible et lorsque les signaux qu'elles émettent les rendent localisables permettant de rameuter d'autres individus.

II/ Implication des processus appris et non-appris dans la réponse aux signaux inconnus

1) L'apprentissage associatif : un processus essentiel

Au cours de cette thèse, j'ai montré que les jeunes sont capables d'associer un signal initialement neutre avec des cris de harcèlement et que le signal neutre provoque des changements de comportement chez les jeunes (**Article 7** ; Figure 8). Ces résultats indiquent que le **processus d'apprentissage associatif** dans le cas du harcèlement est possible chez les jeunes passereaux (voir Magrath et al. 2015b, Potvin et al. 2018 pour des résultats similaires concernant le comportement de fuite). Cette association uniquement basée sur des signaux acoustiques faite dans le nichoir évite un comportement complètement naïf à la sortie du nichoir. Contrairement à l'apprentissage associatif visuel qui peut être complexe dans un milieu dense, les associations acoustiques seraient plus efficaces dans les situations où les tuteurs, les autres proies et les menaces sont difficiles à observer (Potvin et al. 2018, Templeton 2018). Les poussins sont capables d'associer mais cette capacité se révèle-t-elle utile ?

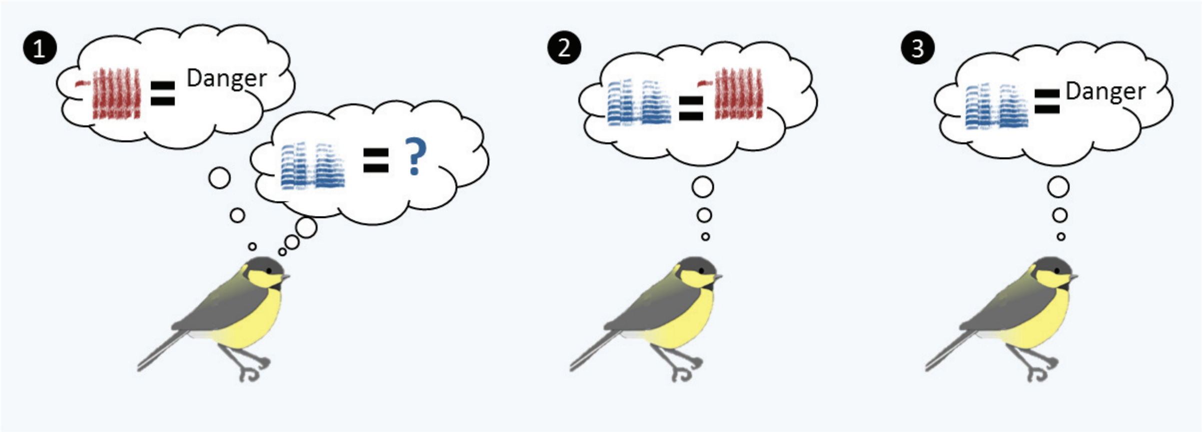


Figure 8 : Comment les jeunes utilisent l'association acoustique pour reconnaitre les menaces. (1) les jeunes mésanges charbonnières associent les cris de harcèlement conspécifiques (rouge) au signal neutre (bleu), mais ne répondent pas initialement au signal neutre. Après association (2), les jeunes répondent au signal neutre car ils le perçoivent comme une menace (3).

L'apprentissage par association est important pour les espèces qui répondent à des cris d'alarmes hétérospécifiques qui diffèrent des cris qui leur sont propres, comme par exemple chez les oiseaux (Hurd 1996, Templeton & Greene 2007), chez les mammifères (Shriner 1998, Fichtel 2004) et lorsque les oiseaux réagissent aux alarmes des mammifères (Rainey et al. 2004) ou que les mammifères réagissent aux alarmes des oiseaux (Müller & Manser 2008). Afin d'optimiser leur réponse, les oiseaux devraient apprendre les signaux de toutes les espèces avec lesquelles ils cohabitent. Néanmoins, ce processus d'association doit être complexe dans le cas où beaucoup d'espèces harcèlent le prédateur. Mon étude montre que 18 espèces harcèlent le prédateur (**Article 2**) et les oiseaux ne sont certainement pas en mesure d'apprendre les signaux émis par toutes ces espèces. Les oiseaux se focalisent peut-être juste sur les espèces qui partagent leur guilde. Par exemple, la mésange noire pourrait apprendre les signaux des roitelets car ces deux espèces se nourrissent au sein de la même niche (i.e. bout de branche).

La variation de la réponse pourrait également être liée à la **densité des espèces** présentent dans la communauté. En effet, il est aussi possible que les variations locales des abondances relatives contraignent plus ou moins fortement les opportunités d'extraire des informations à partir des communications hétérospécifiques. Dans le cas de l'apprentissage par association, plus le nombre d'individus d'une espèce particulière est important, plus les chances d'apprendre le signal acoustique et de répondre seraient élevées. Les regroupements hivernaux composés de plusieurs espèces de passereaux faciliteraient l'apprentissage entre les espèces. Mon travail sur la réponse de deux espèces de mésanges face au troglodyte (espèce solitaire) et à la sittelle (espèce grégaire dans certaines situations) suggère que le contact permanent pendant la période automnale lorsque les espèces forment des regroupements multi spécifiques facilite l'apprentissage des cris de harcèlement. En effet, les mésanges répondent plus à la sittelle qu'au troglodyte (**Article 3**) et une des explications possibles pourrait être que les mésanges entendent plus souvent la sittelle que le troglodyte.

L'apprentissage du harcèlement du prédateur peut être plus facilement mis en œuvre dans le cas des espèces sociales et vivant dans des groupes stables car les individus passent relativement plus de temps ensemble que des individus d'espèces moins sociales qui passent peu de temps avec leur jeunes. Par exemple, les jeunes mésanges volantes passent peu de temps avec leurs parents et le temps durant lequel ils peuvent apprendre à reconnaître un prédateur ou des cris d'alarmes est limité. Dès lors, comment les jeunes oiseaux savent-ils répondre aux cris de harcèlement hétérospécifique ? Une hypothèse est celle d'un apprentissage social des jeunes oiseaux, confrontés à des adultes expérimentés de leur espèce, déjà en interaction avec les hétérospécifiques. Une autre hypothèse est qu'ils seraient attirés de façon innée par le bruit produit par la foule multi spécifique en train d'harceler un prédateur et que, dans leurs premiers contacts avec les hétérospécifiques, ils apprendraient les caractéristiques des signaux des différentes espèces. Une troisième hypothèse est qu'ils seraient attirés par des signaux ressemblant aux signaux intraspécifiques appris dans un premier temps. En accord avec ces deux dernières hypothèses, des études antérieures ont montré que les oiseaux sont sensibles au *pishing*, un son chuintant répété (« psshh ») produit avec la bouche d'un humain présentant certainement des caractéristiques acoustiques similaires aux cris de harcèlement alors que les oiseaux ne le connaissent pas (Zimmer 2000, Langham et al. 2006). Il est important de noter qu'une surexposition à un signal de harcèlement peut entraîner à une perturbation de la séquence comportementale (**Article 7** ; Figure 9). En milieu naturel, les évènements de harcèlement restent rares et la surexposition ne doit altérer ni la sensibilité acoustique ni l'apprentissage du comportement.

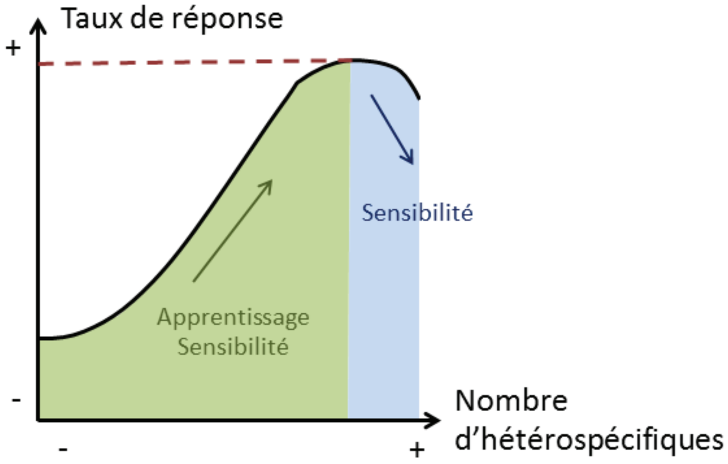


Figure 9 : Taux de réponse d'une espèce A en fonction du nombre d'hétérospécifiques d'une espèce B. Plus le nombre d'hétérospécifiques est élevé plus les chances d'apprendre et de répondre à leurs signaux sont élevées. Un nombre très élevé d'hétérospécifiques pourrait conduire à une surexposition amenant à une diminution de la sensibilité au signal acoustique.

Dans le cas où les espèces sont capables de **mimer et incorporer des signaux d'autres espèces** dans leurs propres répertoires, les réponses entre espèces devraient être facilitées (Wheatcroft & Price 2013). Ce processus d'incorporation faciliterait la communication hétérospécifique lorsque des espèces partagent le même milieu et serait d'autant plus renforcé lorsque les interactions entre espèces sont particulièrement fortes. L'imitation de cris émis par les prédateurs ou les proies hétérospécifiques pourraient également inciter les jeunes à associer ces cris aux cris émis par leur propre espèce (Goodale et al. 2014). Cependant, les capacités d'incorporation d'éléments peuvent varier d'une espèce à l'autre. Par exemple, le pouillot élégant (*Phylloscopus pulcher*) est moins capable d'incorporer les cris d'autres espèces par rapport au pouillot verdâtre (*Phylloscopus trochiloides trochiloides*) car son système de communication est plus simple (i.e. ses cris sont simples et stéréotypés) et moins flexible (Wheatcroft & Price 2013). Les contraintes potentielles liées aux caractéristiques de l'appareil vocal influencent les systèmes de communication chez les vertébrés et on peut s'attendre à ce que ce processus d'incorporation se retrouve principalement chez les oiseaux et rarement chez les mammifères.

Bien que l'apprentissage semble important pour répondre aux cris de harcèlement, dans certains cas, des réponses peuvent se produire sans exposition préalable. Notamment, les vertébrés pourraient ne pas avoir besoin d'apprendre à répondre à des cris hétérospécifiques s'ils pouvaient les identifier uniquement sur la base des similarités acoustiques.

2) Mécanismes impliqués dans les réponses aux cris de harcèlement non appris

a) Réponses des adultes

Dans la mesure où le harcèlement peut être plurispécifique, i.e. associé à plusieurs espèces de prédateurs, on peut s'attendre à ce que les cris de harcèlement élicitent plus de réponses que la présence d'un des prédateurs. Les résultats de notre étude supportent bien cette hypothèse dans la mesure où nous avons pu montrer que dans la zone où la chouette chevêchette n'est pas présente, la réponse aux cris de harcèlement est conservée mais pas celle à la chouette chevêchette (**Article 1**). Ainsi, dans un **environnement multiprédateurs**, les comportements de harcèlement pourraient être maintenus même en l'absence d'une espèce prédatrice spécifique. Cela est probablement particulièrement vrai pour les proies aviaires, étant donné l'omniprésence des prédateurs spécialisés sur les nids.

Dans l'étude des réponses des espèces européennes face à des signaux inconnus émis par trois espèces nord-américaines (**Article 4**), j'ai trouvé d'une part que trois espèces sur quatre répondaient aux signaux inconnus, indiquant que les animaux sont capables de répondre à des cris inconnus **sans expérience au préalable**. D'autre part, mes résultats indiquent une forte variabilité de réponses parmi les espèces de Paridae : pas de réponse de l'espèce de Fringillidé et réponses variables au sein des trois espèces de Paridae. Les analyses de signaux acoustiques couplées aux expériences de repasses révèlent que deux fois sur quatre la proximité structurale des cris de harcèlement est un mécanisme permettant la réponse aux signaux de harcèlement inconnus. Cependant, pour la mésange noire et la mésange bleue, la proximité structurale des cris ne semble pas être un mécanisme expliquant les réponses comportementales. Les capacités cognitives ainsi que la complexité du système de communication de ces espèces pourraient expliquer leurs réponses.

b) Le cas des jeunes passereaux : un certain nombre de questions restent en suspens

Que se passe-t-il dans le cas où les jeunes ne sont pas en mesure de voir les émetteurs des signaux acoustiques ? Plusieurs travaux indiquent que la réponse aux signaux acoustiques repose sur des processus innés et acquis (Haff & Magrath 2012, Haff & Magrath 2013, Barati & McDonald 2017). Mes travaux indiquent que les petits ne distinguent pas un signal de harcèlement d'un signal sans valeur biologique mais que leur réponse à ces deux signaux change avec le temps (**Article 7**). On peut s'attendre à ce que l'expérience des poussins change avec le temps leur permettant ainsi de pouvoir agir de manière appropriée. Comment les jeunes font-ils pour discerner les différents signaux acoustiques qui viennent de l'extérieur ? Pour répondre à cette question, il faudrait émettre différents types de cris d'alarmes mais aussi de chants territoriaux (Barati & McDonald 2017). Les jeunes arrivent-ils à déchiffrer les informations codées dans les cris ? Une étude surprenante indique qu'ils sont capables d'extraire les informations contenues dans les cris de leurs parents (type de prédateur) et adaptent leur comportement en conséquence (Suzuki 2011). Les jeunes mésanges se tapissent au fond de leur cavité lorsqu'elles entendent un signal d'alarme contenant l'information « corbeau » alors qu'elles sortent immédiatement de la cavité lorsqu'elles entendent un signal de harcèlement contenant l'information « serpent ». Une autre interprétation de la réponse des poussins est cependant possible. En effet, afin d'étudier la réponse des poussins, Suzuki a placé un prédateur devant le nichoir et a attendu que les parents arrivent et alarment autour du nichoir pendant 5 minutes. Si on se penche sur le spectrogramme des cris émis par les adultes envers les serpents, ceux-ci ressemblent fortement aux cris de recrutement émis pour garder le contact entre partenaires sexuels (Suzuki et al. 2016) mais également aux cris que les parents émettent pour encourager les petits à sortir du nichoir le jour d'envol (observations personnelles). Etant donné que les tests ont été réalisés « un jour avant la date du jour d'envol » il se peut que les poussins n'aient pas compris « serpent » mais « sortez ». D'ailleurs, je n'ai jamais observé ce phénomène de fuite après diffusion de cris de harcèlement pendant 1 minute sur 38 nichoirs. Bien que les cris de harcèlement utilisés dans mon étude n'aient pas été enregistrés lors d'un évènement de harcèlement envers un serpent, je pense que cette capacité de décodage de l'information n'est pas généralisable.

III/ Un système de communication performant au sein de la communauté des proies

1) Émettre des cris de harcèlement : un moyen pour rassembler les conspécifiques et hétérospécifiques

Cette thèse a contribué à améliorer les connaissances sur les relations entre les proies lors d'un évènement de harcèlement du prédateur. L'utilisation d'approches individuelles fournit des informations sur les facteurs jouant sur la variabilité au risque de prédation.

L'une des particularités des réponses au cri de harcèlement est qu'elle s'insère dans un réseau de communication hétérospécifique. En effet, les réponses élicitées par les cris de harcèlement ne concernent pas seulement les congénères mais aussi un grand nombre d'individus hétérospécifiques (Marler 1957, Klump et Shalter 1984, Francis et al. 1989, Templeton & Greene 2007). Dans notre étude, la séquence utilisée était composée de cris de harcèlement émis par quatre espèces et a sollicité la réponse de treize autres espèces au moins une fois sur les 35 tests effectués (**Article 1**). A partir de ces résultats il n'est évidemment pas possible de ségréger le rôle de la communication intraspécifique de celui de la communication hétérospécifique dans la réponse des quatre espèces présentes sur la bande son. En revanche pour être plus précis il faut faire des tests par binômes. Les tests réalisés par paires d'espèces indiquent que la réponse aux conspécifiques est généralement plus élevée que celle envers les hétérospécifiques (**Article 4**). Les mésanges (**Article 4**) sont les espèces qui participent le plus au harcèlement et elles peuvent ainsi être classées d'**espèces clés**. Ces espèces clés peuvent être considérées comme des espèces « sentinelles », car elles sont les plus communes et pourraient alerter un grand nombre d'espèces de la communauté qui sont particulièrement attentifs à leur comportement anti-prédateur (Templeton & Greene 2007). Leur forte propension au harcèlement combiné à un système de communication complexe font des **Paridés** un groupe particulièrement intéressant pour l'étude de cette stratégie anti-prédatrice. La façon dont les mésanges codent la menace dans leurs cris de harcèlement varie d'une espèce à l'autre (Carlson et al. 2017a). Il serait maintenant particulièrement intéressant de comprendre les raisons pour lesquelles ces différentes espèces utilisent différentes façons pour coder l'information sur la menace. Les mésanges présentent également l'avantage d'être communes sur plusieurs continents permettant ainsi d'étudier comment différents écosystèmes, structures communautaires et populations de prédateurs affectent les stratégies anti-prédatrices et les systèmes de codages de l'information.

Dans la grande majorité des cas les proies rameutent à la fois des conspécifiques et des hétérospécifiques. Cette règle s'applique bien chez les oiseaux mais semble moins générale chez les mammifères. En effet, mêmes si des phénomènes de communication interspécifiques ont été observées chez des espèces de mammifères terrestres (e.g. Gautier-Hion & Tutin 1988, Passamani 1995, Wilcox et al. 2016) comme chez le gibbon à barbe blanche (*Hylobates albibarbis*) et le semnopithèque rubicond (*Presbytis rubicunda*) face à la panthère nébuleuse (*Neofelis diardi*) (Wilcox et al 2016), plus de la moitié des mammifères qui mettent en place cette stratégie vivent en groupe sociaux stables. C'est le cas par exemple des suricates (Graw

& Manser 2007), des tarsiers spectres (*Tarsius spectrum*) (Gursky 2006) ou des éléphants (McComb et al. 2011) qui développent un système de communication intraspécifique. Cette stabilité assurerait un nombre d'individus assez important et assurerait la réciprocité entre les individus dans le cas d'un évènement de harcèlement.

2) Une large bande de fréquence : un moyen universel pour localiser l'émetteur mais imposant des coûts

a) Un phénomène de convergence des signaux acoustiques

Le bénéfice principal du harcèlement (i.e. fuite du prédateur) étant lié au nombre de participants, les cris de harcèlement des différentes espèces devraient se ressembler pour pouvoir échanger des informations de manière efficace (Marler 1955, Johnson et al. 2003). Pourtant il ne semble pas avoir de langage universel car tout le monde ne répond pas à tout le monde (**Article 4**). Mes résultats indiquent que trois espèces de mésanges répondent à des signaux inconnus (**Article 4**) indiquant qu'il y a bien un mécanisme sous-jacent expliquant la réponse.

Au cours de mon travail comparant les cris de harcèlement émis par 23 espèces de passereaux appartenant à 9 familles (**Article 5**), j'ai montré qu'un processus de **convergence** contraint un paramètre acoustique chez toutes les espèces : **la largeur de bande de fréquence**. Ce paramètre acoustique est essentiel pour la **localisation de l'émetteur** (Aubin & Jouventin 2002). En intégrant cette composante dans leurs cris, les oiseaux valident deux des contraintes majeures associées au harcèlement : être localisable et rameuter d'autres individus pour chasser efficacement le prédateur. Un tel processus de convergence n'a, à ma connaissance jamais été étudié chez les différentes espèces de mammifères.

b) La localisation impose des coûts

Les signaux de harcèlement peuvent orienter le prédateur (Krams 2001) et peuvent être coûteux car ils sont localisables et indiquent la position des proies à des prédateurs ou parasites de couvées potentiels (Krama & Krams 2004, Krams et al. 2007). Dans mon cas, même si cela reste anecdotique, il est aussi possible que certaines espèces n'utilisent pas de la même façon les informations véhiculées par les cris de harcèlement hétérospécifiques. Par exemple, Hurd (1996) suggère que le geai bleu (*Cyanocitta cristata*) est attiré par les cris de harcèlement de la mésange à tête noire (*Poecile Atricapillus*), non pas pour venir harceler le prédateur, mais pour s'inviter au repas. Dans mon cas, le geai des chênes (*Garrulus glandarius*), une espèce connue pour être charognard, est venu à la repasse de cris de harcèlement de quatre espèces 2 fois sur 19 (données non publiées).

Dans certains cas le receveur du signal et utilisateur de l'information n'était pas un prédateur mais une proie hétérospécifique potentielle. J'ai souvent entendue des bouvreuils pivoine (*Pyrrhula pyrrhula*) après la repasse de prédateur et des cris de harcèlement alors qu'ils ne s'approchaient jamais du haut-parleur. **L'écoute des cris d'alarmes** présente deux avantages pour les proies potentielles. Tout d'abord, dans un milieu complexe comme la forêt mixte dans laquelle se trouve cette espèce, l'utilisation des indices acoustiques se relève plus efficace que les indices visuels pour connaître la présence d'un prédateur. Deuxièmement, l'*eavesdropping* permet de détecter des prédateurs dans des endroits difficiles à surveiller et permettrait aux bouvreuils de repérer les prédateurs qu'ils ne seraient pas en mesure de détecter. Il existe probablement des coûts énergétiques associés à ce comportement d'effort de vigilance mais ils restent probablement très faibles par rapport au budget énergétique journalier. Pour une espèce d'iguane (*Oplurus cuvieri cuvieri*) il serait avantageux d'évaluer la situation en adoptant un comportement de vigilance lorsque le Tchitrec malgache (*Terspsiphone mutata*) harcèle leur prédateur (Ito & Mori 2009).

3) Un système de (dé)codage hors du commun

a) Les oiseaux peuvent-ils composer des séquences ayant un sens en combinant des appels spécifiques dans des combinaisons guidées par des règles ?

Le codage de l'information dans les cris de harcèlement s'intègrent dans un système de communication complexe. Ce système fait intervenir des structures du signal qui alertent d'un danger immédiat et provoque des comportements de vigilance chez le récepteur alors que d'autres facilitent la localisation de l'émetteur.

Mes résultats indiquent que les cris de harcèlement de la mésange charbonnière reposent sur une **combinaison de deux types d'appels** : un cri d'alarme (motif FME) et un appel de recrutement (motif D) (**Article 6**). Bien que n'ayant pas quantifié avec précision ni le contexte ni la proportion dans lesquels les mésanges charbonnières émettent chacun de ces motifs séparément, mes observations sur le terrain indiquent qu'ils peuvent tous deux être émis isolément. Le cris d'alarme est émis lorsque l'émetteur détecte un danger potentiel et provoque chez le récepteur un comportement de vigilance, l'appel de recrutement est émis pour maintenir une cohésion avec le(s) partenaire(s) social(aux) et provoque le ralliement du récepteur. Une séquence naturelle de cris de harcèlement, c'est-à-dire constituée des cris FME suivi de notes D, provoque à la fois les deux comportements chez le récepteur (i.e. vigilance et ralliement). Lorsque l'on inverse l'ordre des motifs dans la séquence (i.e. D-FME), les récepteurs restent attirés par l'émetteur mais ne manifestent alors plus de vigilance. Ainsi, ces résultats indiquent que les mésanges utilisent l'ordre des notes dans la séquence pour communiquer avec leurs congénères.

Il est actuellement débattu si l'ordre des appels spécifiques composant une séquence doit influencer la signification de la combinaison pour que celle-ci soit définie comme syntaxique. Dans de nombreuses langues humaines, l'ordre des mots dans une phrase n'est pas essentiel pour comprendre le sens de la phrase, bien que dans ces cas, les relations entre les mots sont souvent codées avec des marqueurs grammaticaux (Kaiser & Trueswell 2004, Bolhuis et al. 2018). Il semblerait donc que l'influence de l'ordre d'appel sur la signification de la combinaison ne soit pas déterminante pour affirmer qu'une combinaison est syntaxique ou non. Selon Suzuki et al. (2018), une phrase à deux mots a généralement une signification non ambigüe et, dans de nombreux cas, l'ordre des mots est important pour produire une signification composée. Par exemple, "être vigilant" a une signification sans ambiguïté, alors que la combinaison inversée "vigilant être" a une signification ambigüe et peu claire. Face à ces deux séquences, les humains devraient réagir à la première phrase, mais pas à la seconde car elle ne respecte pas les règles syntaxiques. C'est ce que nous avons observé chez les mésanges : les combinaisons des appels FME et D provoquent des réponses composées que lorsqu'ils sont ordonnés en séquences FME-D.

Les cris de harcèlement ayant la particularité de rameuter un grand nombre d'hétérospécifiques, l'utilisation de la syntaxe comme système de décodage par les hétérospécifiques est-elle possible ?

b) Les règles de décodages varient-elles entre les espèces ?

A ma connaissance, les scientifiques ne savent pas si les espèces utilisent la syntaxe comme système de décodage pour extraire des informations des cris de harcèlement émis par les hétérospécifiques. Les résultats que j'ai obtenus chez les hétérospécifiques (**Article 6**) indiquent que la mésange noire, contrairement au pinson des arbres, est sensible à la réversion de la séquence des cris de harcèlement de mésange charbonnière, bien qu'elle ne réagisse pas de la même manière que les mésanges charbonnières. Cette différence de réponse pourrait s'expliquer par (i) des différences importantes entre espèces au niveau de l'effort de vigilance basale et (ii) la complexité du système acoustique ; il est assez simple chez le pinson et semble complexe chez la mésange noire (**Article 4**). A ma connaissance, seules trois études portent sur le comportement et les cris de harcèlement de la mésange noire (Shimazaki et al. 2016, Suzuki 2016, Carlson et al. 2017a) et les récentes découvertes indiquent que cette espèce assemblerait une petite dizaine de cris composant une séquence de harcèlement complexe (Carlson et al. 2017a, **Article 4**). Afin de savoir si cette espèce de mésange combine des appels dans ses propres cris de harcèlement, il est nécessaire de réaliser des tests supplémentaires. Il semble donc crucial de s'intéresser aux règles grâce auxquelles les hétérospécifiques utilisent et comprennent les composantes du signal acoustique afin d'obtenir une compréhension précise du système de décodage chez les oiseaux. En ce qui concerne les mammifères, un tel système de codage de l'information dans les cris de harcèlement n'est à ma connaissance pas connue. Des futures recherches sur les vocalisations émises par les animaux et des définitions communes entre linguistes et écologues permettront peut-être de percer les secrets du « langage animal ».

V/ Conclusion et perspectives

1) Notre compréhension de la stratégie anti-prédatrice chez les passereaux

Les travaux exposés dans cette thèse m'ont permis d'analyser les différents maillons de la stratégie de harcèlement du prédateur et du système de communication utilisés par les passereaux. Les travaux que nous avons menés chez 36 espèces de passereaux (1) confirment que la prédation joue un rôle majeur dans la mise en place de cette stratégie (**Articles 1 et 2**), (2) affirment que cette stratégie implique une communication entre espèces (**Articles 1, 3 à 6**), (3) que cette communication interspécifique implique des processus innés et acquis (**Articles 5 et 7**) et (4) montrent que les oiseaux ont recours à une solution acoustique similaire pour augmenter leur chance d'être localisés et ainsi rameuter d'autres individus autour du prédateur (**Article 5**). Les mécanismes impliqués dans les réponses aux signaux hétérospécifiques, qu'ils soient liés à l'apprentissage ou non, et la mesure dans laquelle nos résultats sont généralisables à la communication dans les cas du harcèlement du prédateur restent à déterminer. Enfin, une récente étude a montré que le système de communication dans les cris de harcèlement chez la mésange de Chine (*Parus minor*) est très complexe et que le codage de l'information repose sur un système de syntaxe. Notre travail chez *P. major* (**Article 6**) a montré que cette espèce combine deux types de cris pour composer un signal de harcèlement.

L'ensemble de ces avancées nous oblige désormais à considérer la communication acoustique chez les passereaux en prenant en compte le risque de prédation, les interactions hétérospécifiques et la complexité des signaux acoustiques.

2) Perspectives de recherche en cours de réalisation

Le travail réalisé au cours de ma thèse a montré que les passereaux constituent des modèles extrêmement intéressants pour l'étude de la communication hétérospécifique et les résultats que nous avons obtenus ont généré de nouveaux axes de recherche.

(1) Comment les oiseaux d'une même communauté se répondent-ils entre eux ?

Comme vu tout au long de cette thèse, la stratégie de harcèlement du prédateur implique de la communication entre espèces. Jusqu'à présent aucune étude n'a quantifié avec précision la réponse entre espèces au sein d'une communauté. Ainsi, entre avril et juin 2016, j'ai quantifié la variabilité de réponses entre 8 espèces de passereaux communs (n = 1077). Une analyse préliminaire indique que (1) les espèces répondent en moyenne plus à leur propre espèce qu'aux hétérospécifiques, (2) la mésange noire est l'espèce qui répond le plus aux signaux hétérospécifiques, (3) le troglodyte et le rougegorge sont les espèces qui répondent le moins aux signaux hétérospécifiques et les deux espèces qui suscitent le moins d'attraction (Figure 10).

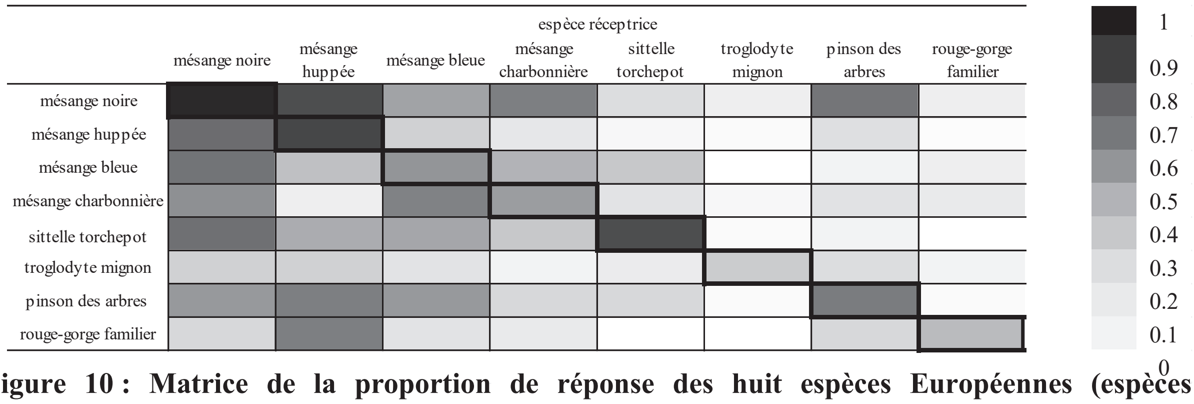


Figure 10 : Matrice de la proportion de réponse des huit espèces Européennes (espèces réceptrice) face aux huit mêmes espèces (n = 1077, contenant 150 tests avec une repasse conspécifique (cellules entourées en gras) et 927 avec une repasse hétérospécifique). L'intensité de la couleur est proportionnelle à la réponse chez chaque espèce (légende à droite de la matrice, 0 correspond à un taux de réponse nul ; 1 correspond à un taux de réponse de 100%).

Pour expliquer les réponses entre ces huit espèces, une analyse prenant en compte la phylogénie des espèces, les distances acoustiques des cris de harcèlement ainsi que leur écologie (la niche alimentaire, la dominance et la grégarité) devrait permettre de comprendre les mécanismes.

(2) L'émission de cris de harcèlement s'accompagne-t-elle de coûts ?

Comme vu précédemment les signaux de harcèlement peuvent être coûteux car ils sont localisables et indiqueraient la position des proies à des prédateurs potentiels (Krama & Krams 2004, Krams et al. 2007). Jusqu'à présent aucune étude ne s'est intéressée aux conséquences indirectes de l'émission quotidienne de cris. Ainsi, au printemps 2017, j'ai élaboré un protocole permettant de mesurer ces coûts en diffusant quotidiennement des cris de harcèlement au niveau d'un nichoir entre le moment où les œufs ont éclos jusqu'à l'envol des poussins. Une analyse préliminaire indique que la croissance des poussins (masse en grammes et longueur du tarse en centimètres; n = 608) n'est pas affectée par diffusion quotidienne des cris contrairement au nombre de poussins qui diminue plus fortement dans les nichoirs traitements que « contrôles » (i.e. nichoirs pour lesquels un signal neutre était diffusé pour remplacer les cris de harcèlement).

(3) Les oiseaux utilisent-ils une règle concernant l'ordre des cris/notes pour décoder une nouvelle séquence de cris/notes ?

Dès le printemps 2016, les capacités de réponse de la mésange charbonnière face à des signaux allopatriques m'a poussé à chercher si cette espèce était en mesure de décoder les informations contenues dans les signaux de mésange à tête noire. J'ai suivi le protocole utilisé dans l'article 7 en mesurant deux comportements : le scan et l'approche de l'individu focal testé lorsque celui-ci était confronté à quatre types de séquence : ABD, D, ABC-D et D-ABC (Figure 11).

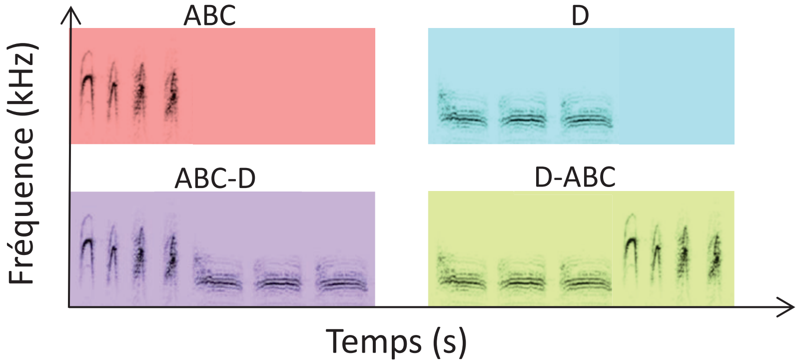


Figure 11 : Spectrogrammes des quatre types de traitements utilisés. Les cris ABC, D et D-ABC a été construite en à partir de la séquence naturelle ABC-D.

Les analyses préliminaires indiquent que la mésange charbonnière ne semble pas utiliser une règle syntaxique pour décoder les cris allopatriques. Le fait d'avoir réalisé nos tests sur des individus en nichoir a peut-être altéré le système puisque les deux comportements mesurés étaient « surexprimés ».

3) Perspectives futures

Outre ces travaux en cours, les études réalisées sur les passereaux tout au long de cette thèse ouvrent plusieurs perspectives de recherche.

a) Amélioration méthodologique : comment mesurer la réponse au harcèlement de manière plus précise ?

Bien que la majorité des chercheurs s'entende sur la question de savoir si une espèce donnée présente un comportement de harcèlement, la description de ce comportement peut varier d'une espèce ou d'un taxon à l'autre. Depuis les premières études descriptives (Altmann 1956, Francis et al. 1989, Zimmermann & Curio 1988), il n'y a eu aucune quantification unifiée de ce comportement. Cela a conduit à un manque de consensus sur la manière d'évaluer et de décrire le comportement de harcèlement entre les espèces et les individus. Il n'existe pas de liste exhaustive décrivant les comportements chez les différentes espèces et les étapes mécanistiques de ce comportement sont très peu décrites (Altmann 1956, Francis et al. 1989, Zimmermann & Curio 1988). Un certain nombre de questions reste en suspens : quels sont les individus ou les espèces qui s'engagent en premier ? Est-ce que tous les individus s'engagent de la même manière ? Est-ce que les individus se relaient ?

Au cours de cette thèse, dans la grande majorité des tests réalisés, j'ai quantifié la réponse des oiseaux à l'aide de la distance au haut-parleur (i.e. je considérais que la réponse était positive si l'oiseau s'approchait dans un rayon de 15 mètres autour du haut-parleur, distance utilisée dans d'autres études e.g. Hua et al. 2016). Bien que le temps d'arrivée et la distance minimale au haut-parleur ne soient pas liés à l'émission de cris de harcèlement (**Article 4**), il me paraît essentiel de mesurer plus précisément la réponse de l'individu focal testé afin d'évaluer avec exactitude l'intensité de la réponse au harcèlement. Je propose un score à attribuer aux individus durant les tests réalisés dans le cas de l'étude du comportement de harcèlement (adapté de Cunha et al. 2017) (tableau 3). Le score, allant de 1 à 10, est croissant. Les valeurs les plus faibles correspondent à une faible intensité de réponse alors que les scores élevés sont attribués aux individus qui harcèlent fortement.

Tableau 3 : Scores à donner aux individus selon leur réponse au signal.

score	distance (m)	émission de cris	mouvements agités	attaque
1	< 15	non	non	non
2	< 15	oui*	oui*	non
3	< 10	non	non	non
4	< 10	oui*	oui*	non
5	entre 5 et 10	oui*	oui*	non
6	entre 2 et 5	non	oui	non
7	entre 2 et 5	oui	oui*	non
8	< 2	non	oui	non
9	< 2	oui*	oui*	non
10	0	oui	obligatoire	oui

*un comportement sur les deux est suffisant. L'individu peut émettre des cris de harcèlement et s'agiter mais aussi émettre des cris et ne pas s'agiter (ou l'inverse).

Le comportement de harcèlement comprend également une combinaison de comportements d'agitation stéréotypés, tels que le battement des ailes (l'oiseau ouvre et ferme rapidement ses ailes en restant posé) et le scanne de l'environnement (i.e. mouvements évidents de la tête où l'oiseau regarde de gauche à droite et de droite à gauche) (Curio 1978, Carslon et al. 2017c). Ces deux comportements, trop peu souvent pris en compte en biologie du comportement, sont cruciaux pour apprécier le comportement dans sa globalité. Le fait d'avoir pu observer sur le terrain des mésanges noires et charbonnières battre des ailes durant une partie des tests réalisés me conforte dans cette idée. Il serait également intéressant de mesurer ces deux comportements chez les individus qui ne répondent pas (i.e. restent ≥15m) afin de connaître leur sensibilité au signal émis. On pourrait ainsi dissocier les individus non sensibles au signal de ceux qui montrent un intérêt et pourraient être classés de « tricheurs ». Toutefois, sur le terrain les choses sont beaucoup plus complexes. En effet, la mesure de ces variables demande un effort de terrain considérable et des heures d'observations sont nécessaires pour étudier et comprendre ces comportements en milieu naturel.

b) Les variations comportementales entre les individus : implications des traits de personnalité ?

Les comparaisons de réponses entre espèces indiquent qu'elles ne répondent pas toutes de la même manière aux cris intraspécifiques et hétérospécifiques. Cette variabilité pourrait être liée à la socialité des espèces. Par exemple, la mésange noire est l'espèce qui répond le plus et vit en groupe alors que les espèces solitaires comme le rougegorge et le troglodyte répondent très peu.

Les tests de réponse au harcèlement répétés sur les mêmes individus occupant les nichoirs que j'ai réalisés au printemps dernier semblent indiquer des variations intraspécifiques (données non présentées). Si les différences de comportement entre les individus sont répétables et héritables, ce trait comportemental ferait partie intégrante du phénotype de personnalité. Depuis quelques années, l'étude de la variabilité individuelle suscite un intérêt considérable de la part de la communauté scientifique. Savoir si un comportement anti-prédateur est reproductible chez un individu, ou s'il change au fil du temps et des circonstances, permettrait de mieux comprendre la souplesse de ce comportement et d'étudier l'importance de certains individus dans l'initiation et le maintien du comportement de harcèlement. L'utilisation d'approches individuelles offrirait de nouvelles perspectives dans l'étude des relations proie-prédateur car cela permettrait d'étudier les processus sous-jacents à la mise en place du comportement de harcèlement.

c) Capacités cognitives et perception de la menace

Les passereaux sont des organismes exceptionnels dotés de facultés d'adaptation, d'orientation, de communication, et même de créativité ! Les récentes découvertes scientifiques font exploser le mythe de la « cervelle d'oiseau » : mémoire spatiale, capacité à utiliser des outils, à se reconnaître eux-mêmes et entre congénères… Les capacités cognitives des oiseaux, englobant les mécanismes par lesquels les individus acquièrent, traitent, stockent et agissent sur l'information provenant de l'environnement seraient liées à la taille du groupe (Ashton et al. 2018). Par rapport à l'approche interspécifique traditionnelle dans l'étude de l'évolution cognitive, qui peut manquer de robustesse parce que la variation des performances cognitives au sein des espèces est souvent considérée comme du " bruit " (Thornton et al. 2014), le fait de se concentrer sur la variation individuelle des performances cognitives permet de quantifier les causes et les conséquences de la variation des capacités cognitives 16-20 (Rowe & Healy 2014, Thornton et al. 2014). Une approche intraspécifique permet également de contrôler les confusions écologiques et phylogénétiques associées aux comparaisons interspécifiques (Thornton & Lukas 2012). À partir de mes résultats et des résultats antérieurs chez les passereaux, l'étape suivante consiste à explorer les indices précis qui déclenchent un comportement antiprédateur au niveau individuel. Il serait intéressant d'étudier par exemple la perception des menaces chez le cassican flûteur (*Cracticus tibicen*), une espèce connue pour son comportement de harcèlement mais aussi pour ses capacités cognitives (Kaplan et al. 2009, Koboroff et al. 2013, Ashton et al. 2018), et particulièrement comment une performance cognitive élevée permet aux individus de réagir de façon appropriée face aux menaces.

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Communiquer entre espèces pour faire face au prédateur: le cas des cris de harcèlement chez les passereaux

Si le signalement du prédateur provoque le plus souvent la fuite des proies, il induit parfois un comportement particulier incitant la proie à s'approcher du prédateur et le harceler pour provoquer son départ plutôt que de se mettre hors de sa portée. Ce comportement de harcèlement s'accompagne de l'émission d'un signal hétérospécifique conduisant de nombreuses espèces à venir harceler le prédateur. L'objectif de mon travail de thèse est de comprendre comment est régi le transfert d'informations entre plusieurs espèces de passereaux dans le cas du comportement de harcèlement d'un prédateur. Mes travaux montrent que le comportement de harcèlement des passereaux face à un rapace nocturne dépend du risque de prédation posé par ce prédateur. Par ailleurs, les résultats indiquent un transfert d'informations entre les espèces et mettent en évidence une propension variable des différentes espèces à se rallier autour du harceleur. Les variations observées dans la réponse aux cris de harcèlement émis par des individus hétérospécifiques peuvent dépendre de la similarité acoustique, des relations interspécifiques et des variations saisonnières. Mes résultats indiquent aussi que la connaissance préalable des signaux de harcèlement n'est pas indispensable pour induire une réponse, même si un processus d'apprentissage associatif favorise sa mise en place. Mon travail suggère également une évolution convergente des cris de harcèlement, générant des signaux dont la structure permet une localisation rapide de l'émetteur, indispensable pour rameuter des proies potentielles lors du harcèlement. L'ensemble de ces avancées nous oblige désormais à considérer la communication acoustique chez les passereaux en prenant en compte le risque de prédation, les interactions hétérospécifiques et la complexité des signaux acoustiques.

Mots clés : attraction hétérospécifique, communication acoustique, comportement de harcèlement, passereaux, stratégie anti prédatrice.

Communication between species to deal with the predator: the case of mobbing calls within passerine birds

Signaling the presence of a predator most often causes the escape of prey, but it sometimes induces a particular behaviour prompting prey to approach and harass the predator to cause his departure. This mobbing behaviour is associated with the emission of signals leading individuals from different species to come harass the predator. The objective of this thesis is to understand how the transfer of information between several passerine species is organized in mobbing behaviour against predators. My work shows that the mobbing behaviour of passerine birds against a nocturnal raptor depends on the predation risk imposed by this predator. In addition, my results indicate a transfer of information between species and highlight a variable propensity of different species to rally around the harasser. The observed variations in the response to heterospecific calls depended on acoustic similarity, interspecific relationships and seasonality. My results also indicate that prior knowledge of harassment signals is not essential to induce a response, even if an associative learning process promotes its implementation. My work also suggests a convergent evolution in mobbing calls, generating signals with a structure that allows the emitter to be quickly located, an essential parameter to rally potential prey during harassment. My thesis consequently shows that to better understand acoustic communication in passerine birds, it is necessary to consider predation risk, heterospecific interactions and the complexity of acoustic signals.

Keywords: acoustic communication, antipredator strategy, birds, heterospecific attraction, mobbing behaviour.

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