Predation as a cost of sexual communication in nocturnal seabirds: an experimental approach using acoustic signals

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Conspicuous behaviour, such as sexual advertisement, exposes animals to predation; mate attraction thus often conflicts with antipredator behaviour. We investigated whether an avian predator, the brown skua, *Catharacta antarctica lönnbergi*, uses the mate attraction calls of colonial seabirds, the petrels. The majority of petrels attract mates at night and vocalizations are their main way of communicating. At our study sites, skua predation on nocturnal petrels was heavy, and concentrated particularly on a single species, the blue petrel, *Halobaena caerulea*. Using playback experiments, we showed that skuas can use male petrel calls as a cue for prey location and selection. This listening behaviour of skuas probably imposes a major constraint on advertising petrels, and especially on single males which face a trade-off between attracting females (which respond by calling in flight) and avoiding predation. We also investigated the consequences of this predation risk on the behaviour of petrels: a second set of playback experiments showed that the most heavily preyed on petrel species could use skua territorial calls to infer predation risk and stop calling thereafter, which may reduce conspicuousness and predation risk.

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Communication involves three elements: a sender individual (emitter), a signal and a recipient individual (receiver). These are connected by an optimizing principle, to make the signal as efficient as possible (Smith 1977; Slater 1983; Bradbury & Vehrencamp 1998). Signal production is costly for the sender, which expects some benefit in return (Slater 1983; Yasukawa 1989). From this point of view, sexual communication is particularly interesting because the benefit, finding a mate, has a direct and obvious fitness component for the sender.

Sexual signals are generally long range and nondirectional in order to be perceived by many potential mates. A third party can thus extract information from a communicative interaction between mates (or future mates) without being directly involved in the interaction (McGregor & Dabelsteen 1996). Such listening behaviour might be by 'illegitimate' receivers such as competitors, parasites or predators (Verrel 1991; Bradbury & Vehrencamp 1998). This situation has often been described for insects, either predators or parasites, that locate their prey or hosts with acoustic signals (e.g. Hoy 1992; Robert et al. 1992; Höglund 1993; Römer 1993; Heller 1995; Wagner 1996) or visual signals (Lloyd 1981; Wing 1988). It has also been found in fish (predators using visual signals: e.g.

Endler 1983, 1991) and amphibians (bats using acoustic signals: e.g. Ryan et al. 1981, 1982; Tuttle & Ryan 1981). In birds, the majority of studies have focused on predation risk according to plumage brightness and conspicuousness (e.g. Promislov et al. 1992; Andersson 1994; Götmark 1997). Acoustic communication is also important: vocalizations and nonvocal sounds are used for territory establishment and defence, mate attraction, pair bond maintenance and parent–offspring relationships (Kroodsma & Miller 1982; Searcy & Andersson 1986; Kroodsma & Byers 1991; Catchpole & Slater 1995). However, there is no observational or experimental evidence of a parasitic use of sexual acoustic signals by a predator in birds.

In colonially breeding birds, constraints on acoustic communication are expected to be maximal (e.g. Bretagnolle 1996). This arises from increased intrasexual competition for access to mates in a colonial context (Wittenberger & Hunt 1985) leading to more conspicuous and informative signals (Andersson 1994). As mentioned above, conspicuous signals may attract the attention of heterospecific 'parasites', such as predators (Verrel 1991; Arak & Enquist 1993). Several predators concentrate and specialize on bird colonies, which represent locally abundant and predictable prey (e.g. Wittenberger & Hunt 1985; Siegel-Causey & Kharithonov 1990). Coloniality might then impose conflicting constraints on communication and, having highly detectable signals, may be a risky strategy.

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The vast majority (ca. 92%) of procellariiform seabirds (families Procellariidae, Pelecanoididae and Hydrobatidae, hereafter referred to as petrels) are nocturnal on their breeding grounds (Warham 1990, 1996; Del Hoyo et al. 1992). All petrels are colonial and many species breed on sub-Antarctic islands (Warham 1990, 1996). On the majority of these, nocturnal burrow-dwelling petrels are heavily preyed on by *Catharacta* skuas (see Mougeot et al. 1998 for a review), which concentrate locally on petrel colonies. Predation by skuas at petrel colonies occurs at night, when petrels are active at the colony, and mostly on the ground, as petrels have poor mobility on land (Furness 1987; Young et al. 1988). In response to predation pressure, petrels are expected to have developed antipredator behaviour. Nocturnality, for example, may have evolved in response to predation (Bretagnolle 1990a; Brooke & Prince 1991; McNeil et al. 1993). The majority of species studied so far also reduce their activity on land on moonlit nights (see Bretagnolle 1990a; McNeil et al. 1993 for reviews), which may be an additional antipredator strategy in response to an increased predation risk (Bretagnolle 1990a; Watanuki 1986; Mougeot & Bretagnolle, in press).

As petrels are nocturnal on their breeding colonies, they cannot communicate by sight (Bretagnolle 1996). We therefore suspected visual cues to be of little use for prey location or predator avoidance (except on moonlit nights, when foraging success of skuas increases: Mougeot & Bretagnolle, in press). Olfaction, although well developed in some species, also does not seem to be used for communication (Bretagnolle 1996), but rather for foraging (Lequette et al. 1990; Verheyden & Jouventin 1994) or nest location (Grubb 1974). Vocalizations are certainly the main and perhaps the only way of communicating at colonies of nocturnal petrels (Bretagnolle 1996), and petrel calls are already known to have territorial and sexual functions (James & Robertson 1985; Brooke 1986, 1990; Genevois & Bretagnolle 1995; Bretagnolle et al. 1998). We chose, therefore, to conduct playback experiments to investigate whether the brown skua, *Catharacta antarctica lönnbergi*, exploits the acoustic signals used in mate attraction by petrels. We first showed experimentally that this specialist predator can use petrel vocalizations to locate and catch them, and that call attactiveness matched the incidence of the species in the diet of skuas. We then investigated the consequences of the predator's hunting behaviour on the calling activities of the prey. Silence is a common defence against listening predators, and we used playback experiments to test whether petrel species can detect the predator by its calls, and reduce their own vocal activity accordingly.

METHODS

Study Areas

We conducted this study during the austral summers of 1993 and 1994, on Mayes and Verte islands, in the Kerguelen archipelago (48°28′S, 69°57′W), where brown skuas feed almost exclusively on nocturnal burrow-nesting petrels.

Mayes Island (2.3 km^2) has dry soils and is densely vegetated, providing diverse and highly suitable breeding sites for burrow-dwelling petrels (Weimerskirch et al. 1989). Twelve petrel species breed there in large numbers (several hundred thousands of pairs; see Mougeot et al. 1998) and at high densities with up to six burrows/m^2 in some areas (unpublished data). Three species are particularly abundant on breeding colonies, and are present in similar numbers: blue petrel, *Halobaena caerulea*, thin-billed prion, *Pachyptila belcheri*, and the common diving-petrel, *Pelecanoides urinatrix* (Weimerskirch et al. 1989; Mougeot et al. 1998). As their food is abundant, the brown skua population is especially numerous on Mayes Island (85 breeding pairs), and the density is ca. 110 skuas/km^2, including nonbreeders (Mougeot et al. 1998). Skuas feed mainly on the blue petrel (73% of diet), the thin-billed prion (19%) and the common diving-petrel (3.5%). About 50 000 petrels are killed by skuas each year on this island (Mougeot et al. 1998).

We conducted additional fieldwork on Verte Island to study other petrel species. This island is smaller than Mayes Island (1.5 km^2), and its vegetation and associated soils have been intensely degraded by rabbits, *Oryctolagus cuniculus*. Consequently, the petrel community is poorer than that of Mayes Island, with only eight breeding species and fewer overall breeding numbers. The most abundant species are blue petrel, Antarctic prion, *Pachyptila desolata*, and South Georgia diving-petrel, *Pelecanoides georgicus*. Density of brown skuas is also lower, with one nonbreeding and six breeding pairs in 1993–1994 (ca. 9 skuas/km^2). Skuas there feed mostly on the blue petrel (88% of diet), the Antarctic prion (5%) and the South Georgia diving-petrel (4%; Montcorps et al. 1998).

Playback Experiments with the Predator

We used playback experiments to simulate a petrel calling from the ground. We studied the responses of brown skuas to playback calls of 10 species: eight were from petrel species breeding on the study areas (the blue petrel; thin-billed and Antarctic prions; common and South Georgia diving-petrels; Wilson's storm-petrel, *Oceanites oceanicus;* grey-backed storm-petrel, *Garodia nereis;* and black-bellied storm-petrel, *Fregetta tropica*), and two were control bird species, whose vocalizations were unknown to skuas (the Manx shearwater, *Puffinus puffinus,* and the chaffinch, *Fringilla coelebs*).

Petrel calls are species specific, that is, calls are much more variable between than within species (Bretagnolle 1996; Warham 1996; see also sonagrams in Fig. 1). All petrel playbacks were of male calls, as males are potentially more vulnerable to skuas than females (Mougeot & Bretagnolle, in press). We recorded on Kerguelen all calls used in playbacks (except for control species, whose calls were recorded in France), by placing the microphone within the burrow, so that background noise was kept minimal (it was not detectable on sonagrams), and similar for all tapes. For each species, calls from three to five different males were mixed on the same endless tape, to take into account intraspecific variations in male calls (but see below for statistical analysis). Calling rate in
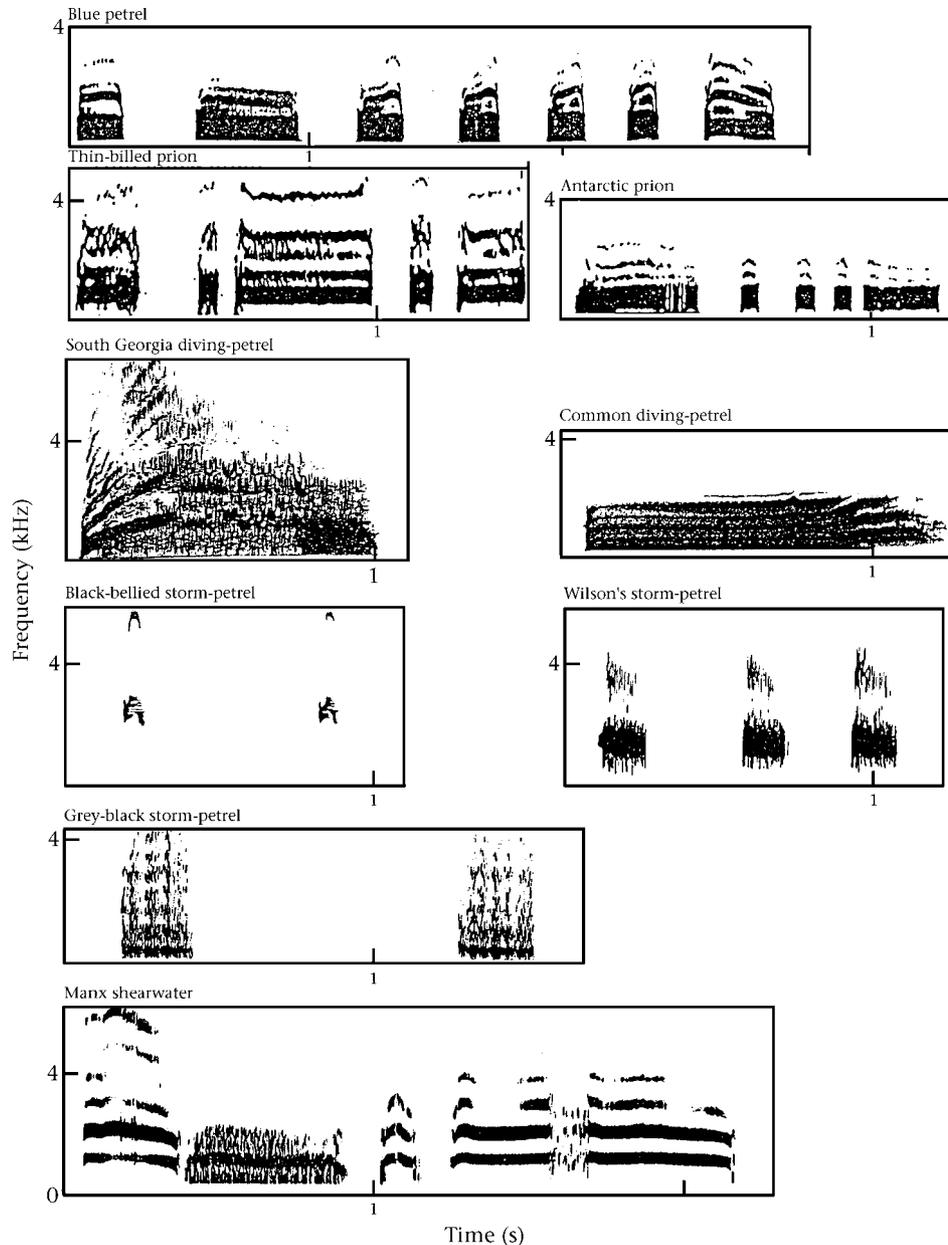
Figure 1. Sonagrams of the male petrel calls used for the playback experiments conducted on brown skuas. They were produced on a Kay 6061B Sonagraph with wideband filter (300 Hz).

endless tapes matched that of natural calls. For playbacks, we used a Sony TCD5 tape recorder connected to a 4-W speaker that was hidden in the vegetation and could not be detected visually, thus mimicking a petrel calling close to its burrow. Sound loudness matched that of natural calls, and was kept constant for all tests.

All tests were done by the same observer either during the day, or at night when moonlight allowed observation of skuas. The loudspeaker was placed within a skua territory, and its responses were observed at a distance with $\times$ 10 binoculars. During an experimental session, we exposed the skua to 1 min of a playback, the species being randomly chosen from the 10 test calls. The initial distance (m) between the skua and the loudspeaker was

estimated visually for each test. We recorded skua responses to playbacks as follows: (1) no reaction (i.e. bird resting or preening); (2) looking towards loudspeaker, head upright; and (3) approach loudspeaker (on ground or, more rarely, in flight). If the skua did not respond, we exposed it, after at least 1 min of silence, to 1 min of another playback call, randomly selected from the nine remaining test calls. An experimental session ended when the skua showed a response or, if no response occurred, after playback of five different test calls.

We did 718 playback tests during this study. These were conducted on 42 skuas (15 pairs from Mayes Island and six pairs from Verte Island), identified from their plastic bands on Mayes Island, or from their territory and sex on
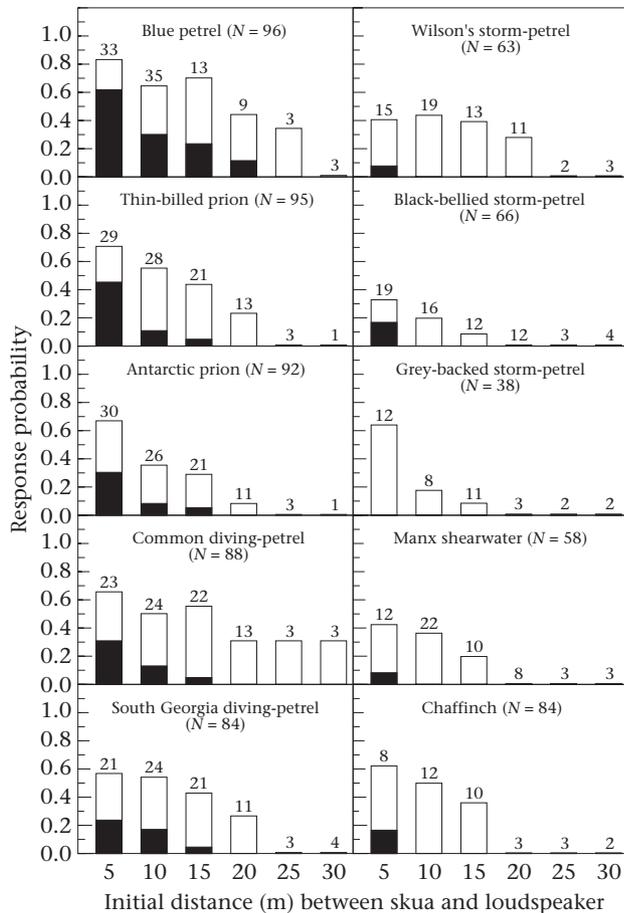
Figure 2. Response probability of brown skuas to the 10 playback calls according to initial distance between skua and loudspeaker. □ All responses; ■ approach responses. Sample sizes above histograms refer to number of tests.

Figure 3. Mean±SE observed probability of response (○) and approach (●) of brown skuas to the playback calls of nine petrel species and chaffinch, regrouped into five prey categories: (1) nonprey; (2) rare prey; (3) occasional prey; (4) secondary prey; (5) main prey. Playbacks: CHA: chaffinch; MSH: manx shearwater; GBSP: grey-backed storm-petrel; BBSP: black-bellied storm-petrel; WSP: Wilson's storm-petrel; SGDP: South Georgia diving-petrel; CDP: common diving-petrel; TBP: thin-billed prion; AP: Antarctic prion; BP: blue petrel. Sample sizes above plots refer to number of skuas tested.

Verte Island (females are noticeably larger than males; Furness 1987). We conducted two to five sessions per skua, with at least a 5-day interval between two consecutive sessions. We used the whole data set (N=718 tests) to describe skua responses to playbacks (samples sizes are given in Fig. 2 for each playback separately). To avoid pseudoreplication, we used a restricted data set for the statistical analyses, keeping only one test per individual skua and per playback (the first conducted with a given petrel species on a given skua). Sample size for the statistical analyses thus included 340 tests, with 28 or 40 tests per playback (not all skuas were tested with all playbacks; see sample sizes in Fig. 3). Skuas never approached in response to grey-backed storm-petrel playback calls, so this species was removed from the analyses conducted on skua approach probability.

Playback Experiments with the Prey

We conducted playback experiments to investigate whether petrels used auditory cues (i.e. skua territorial calls) for predator detection and avoidance. We studied seven petrel species on t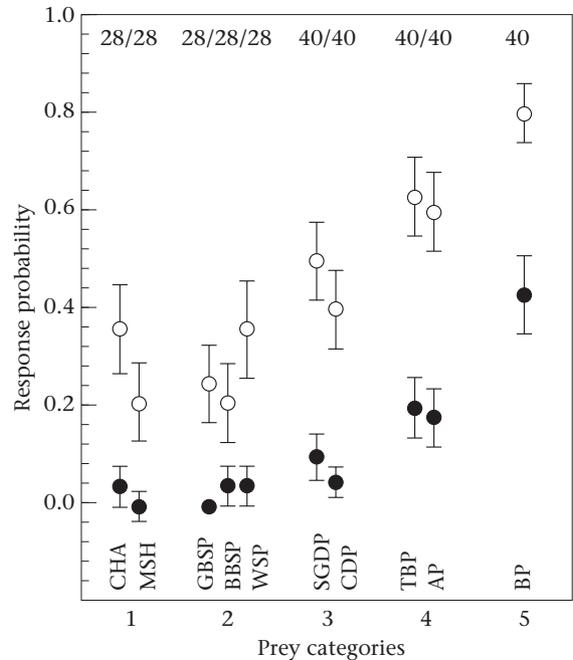he two study areas: five petrel species breeding on Mayes Island (blue petrel, thin-billed prion, common diving-petrel, white-headed petrel, *Pterodroma lessonii*, and Wilson's storm-petrel) and three species breeding on Verte Island (blue petrel, Antarctic prion and South Georgia diving-petrel). We counted petrel vocalizations at colonies at night during periods of silence (controls) and during playback calls of brown skua. In addition to skua playback, two controls were used: kelp gull, *Larus dominicanus* (a close relative of the skua, which breeds on the study sites but does not feed on petrels) and the chaffinch (whose vocalizations are unknown to petrels). Each test lasted 22 min and was organized as follows: silence (5 min)/playback 1 (2 min)/ silence (3 min)/playback 2 (2 min)/silence (3 min)/ playback 3 (2 min)/silence (5 min). Six playback tapes were prepared, each containing the skua and two control playbacks but differing in the order in which they were performed, and were used in succession for the different tests. The loudspeaker was placed on the ground, pointing towards the sky, and the observer sat 5 m from it to record the vocal activity of study petrels in a 10-m radius around him. We did tests at different, randomly selected, colony sites. Calls uttered from the ground or in flight, by males or females, were counted separately during periods of silence and playbacks, and are presented as number of calls/min for each petrel species.

Table 1. Results of the logistic regressions testing for between- and within-prey category differences (species nested within each prey category) in the probability of response and approach by skuas to playbacks

Dependent: Source	Response probability			Approach probability*		
	df	χ^2	P	df	χ^2	P
Intercept	1	39.07	<0.0001	1	2.57	0.11
Distance†	1	46.70	<0.0001	1	28.07	<0.0001
Between-prey categories‡	4	23.41	<0.0003	4	26.34	<0.0001
Within-prey categories§						
Non prey	1	0.09	0.76	1	0.00	0.99
Rare prey	2	1.72	0.35	1	0.02	0.88
Occasional prey	1	0.36	0.55	1	0.28	0.59
Secondary prey	1	0.00	0.95	1	0.28	0.59
Likelihood ratio**	46	43.77	0.57	41	8.09	1.00

CATMOD Procedure, maximum likelihood analyses (SAS 1988), $N=340$ tests.

*Skuas never approached in response to playbacks of grey-backed storm-petrel, so this species was excluded for the analysis of approach probability ($N=312$ tests).

†Distance between skua and loudspeaker at the beginning of the test (regressor).

‡Nonprey: controls; rare prey: storm-petrels; occasional prey: diving-petrels; secondary prey: prions; main prey: blue petrel.

§Petrel species and chaffinch nested within each prey category, separately.

**The likelihood ratio is given as a goodness of fit of the model; the chi-square value allows a test of the null hypothesis that the model does not differ from the data, the df corresponding to the population size used for the analyses. For each parameter included in the model, chi-square values allow a test of the null hypothesis of an absence of effect of the variable, the df corresponding to the number of classes for each variable.

Statistical Analyses

We used the SAS 6.11 statistical package (SAS 1988). For the experiments with skuas, we used logistic regressions (Catmod procedure, maximum likelihood analyses) to assess whether response and approach probabilities differed between prey species, according to their local incidence in the diet of skuas (available from Montcorps et al. 1998; Mougeot et al. 1998). We thus regrouped the 10 petrel species and the chaffinch into five prey categories: (1) nonprey: the two control species; (2) rare prey: the three storm-petrel species (<1% of diet); (3) occasional prey: the two diving-petrel species (3–4% of diet); (4) secondary prey: the two prion species (5–20% of diet); and (5) main prey, the blue petrel (>70% of diet). The initial statistical models systematically included the distance between skua and loudspeaker at the beginning of the test, the prey categories and the species nested within each prey category, to test for between- and within-prey category differences in the skuas' response to playbacks.

For the experiments with petrels, we tested for each petrel species separately whether vocal activity differed between the counts of the seven treatments (i.e. the four silent controls and the three playbacks), using Friedman tests for repeated measures. If a significant difference was found, we then used post-hoc tests (Wilcoxon signed-ranks tests for paired samples) to compare vocal activity levels between pairs of counts. If playbacks of skua calls had a significant effect on a given petrel species, we further investigated which individuals reduced their vocal activity. We tested for a difference in calling rate between playbacks and silent controls for each sex and calling context (ground versus in-flight calling), using Wilcoxon signed-ranks tests for paired samples. We also

investigated whether one sex reduced calling activity more than the other, testing for a between-sex difference in the reduction of calling rate in response to playbacks (calculated as the calling rate difference between playbacks and silent controls, in percentage of the vocal activity during silent controls). All statistical tests are two tailed. When multiple tests were performed on the same data sets, we applied a sequential Bonferroni correction and present only significant results after correction.

RESULTS

Predator Responses to Prey Playback Calls

The probability that a skua responded to the calls of a given petrel species (either by a head upright or an approach) depended strongly on the distance between the skua and the loudspeaker at the beginning of the test (see Fig. 2 for data, Table 1 for statistical tests). Differences in skua responses were tested between prey categories, with the playback species nested within each prey category. Skua responses differed significantly between prey categories, but not within each prey category (Table 1, Fig. 3). Although playback rank during a given session could have had some effect, that is, a fifth playback could have elicited more (or less) response than a first playback, this was not the case, as there was no significant effect of test rank on response probability (logistic regression: $\chi^2_1=0.77$, $N=340$, $P=0.38$) or approach probability ($\chi^2_1=0.60$, $N=312$, $P=0.44$).

To define between-prey category differences, we tested for differences in approach probability (the highest response level of skuas) between pairs of prey categories, using the same logistic regression models (Table 2, Fig. 3).

Table 2. Results of the logistic regressions conducted with pairs of prey categories to test for between-prey category differences in the probability of an approach response by skuas to playbacks (see also Table 1)

Prey categories	Source*	df	χ^2	P
Nonprey/rare prey	Distance	1	7.81	<0.006
(controls/storm-petrels)	Between-prey categories	1	0.64	0.43
	Likelihood ratio	17	2.30	1.00
Rare prey/occasional prey	Distance	1	6.96	<0.009
(storm-petrels/diving-petrels)	Between-prey categories	1	0.99	0.32
	Likelihood ratio	22	2.31	1.00
Occasional prey/secondary prey	Distance	1	16.98	<0.0001
(diving-petrels/prions)	Between-prey categories	1	4.91	<0.03
	Likelihood ratio	17	3.74	0.99
Secondary prey/main prey	Distance	1	18.80	<0.0001
(prions/blue petrel)	Between-prey categories	1	8.87	<0.003
	Likelihood ratio	16	1.91	1.00

*The intercept was not significant and was removed from all models.

The probability of approach did not differ significantly between playbacks of nonprey (controls) and rare prey (storm-petrels), nor between playbacks of rare and occasional prey (diving-petrels). Conversely, approach probability was significantly higher for playbacks of secondary prey (prions) than for those of occasional prey. Approach probability was also significantly higher for playbacks of the main prey (blue petrel) than for those of secondary prey, for playbacks of secondary prey than for those of nonprey (controls) or rare prey (storm-petrels), and for playbacks of the main prey than for those of nonprey, rare or occasional prey (logistic regression models as in Table 2, all $P<0.05$ for prey category effects). Attractiveness of petrel calls to skuas, as measured by approach responses to playbacks, thus differed between petrel species and matched the incidence of the petrel species in the diet of skuas.

Prey Responses to Predator Playback Calls

Total vocal activity (calls/min) did not differ significantly between the seven treatments (four silent controls and three playbacks) for the South Georgia diving-petrel, the white-headed petrel and the Wilson's storm-petrel (Friedman test for repeated measures: $\chi^2_6=5.4$, 5.7 and 6.8, respectively, all $P>0.25$; Fig. 4), indicating that playbacks of predator calls had no significant effect on the vocal activity of these petrel species. In contrast, vocal activity differed significantly between counts for the blue petrel, the thin-billed and Antarctic prions, and the common diving-petrel ($\chi^2_6=30.5$, 26.3, 24.4 and 30.3, respectively, all $P<0.001$). Post hoc tests showed that, in these four species, calling rate did not differ significantly between silent controls, nor between silent controls and playbacks of kelp gull or chaffinch calls (Wilcoxon signed-ranks test for paired samples: all $P>0.10$; Fig. 4). In contrast, vocal activity was significantly lower during playbacks of skua calls than during corresponding silent controls or playbacks of kelp gull or chaffinch calls (Fig. 4). In these four species that reduced calling activity during playbacks of skua calls, we further investigated which class of birds was
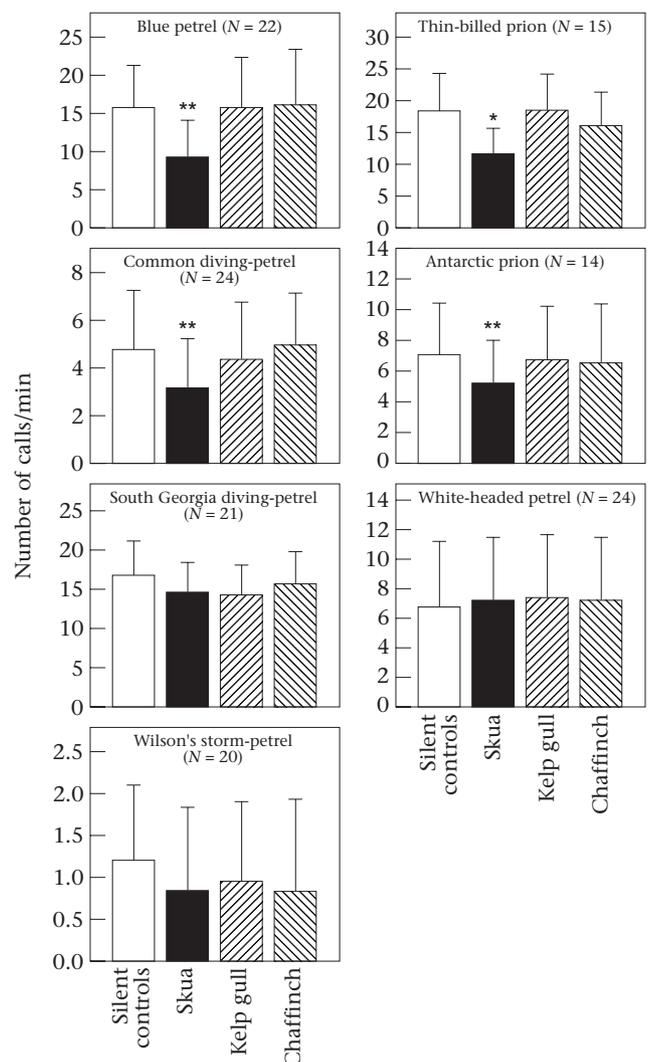

Figure 4. Vocal activity ($\bar{X}\pm$SD number of calls/min) of study petrels during silent controls and during playbacks of brown skua, kelp gull and chaffinch. Sample sizes (number of playback tests) are given in parentheses for each species. (Wilcoxon signed-ranks tests: *$P<0.01$; **$P<0.001$.
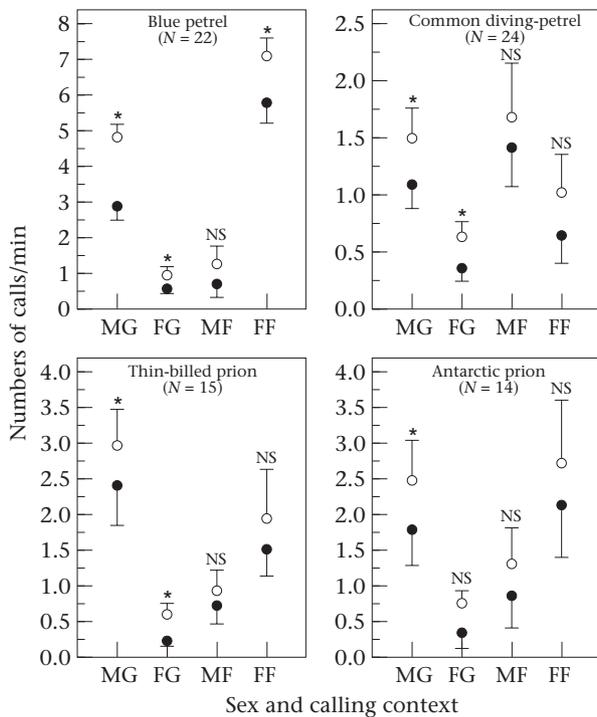
Figure 5. Vocal activity ($\bar{X} \pm SE$ number of calls/min) of study petrels during silent controls (○) and during playbacks of brown skua (●) according to sex and calling circumstance (MG: males on the ground; FG: females on the ground; MF: males in flight; FF: females in flight). Sample sizes are given in parentheses for each species and are the same for each sex and calling circumstance. (Wilcoxon signed-ranks tests: significance levels after sequential Bonferroni correction: *$P<0.0125$; **$P<0.00125$; NS: $P>0.0125$).

most strongly affected. We found that ground calling was significantly reduced by both sexes in all species except the Antarctic prion (in the latter, only males significantly reduced ground calling activity; Fig. 5). For blue petrel, the reduction of ground calling was greater in males than in females (Wilcoxon signed-ranks test: $|Z|=3.49$, $N=22$, $P<0.005$; Fig. 5), whereas no between-sex differences were found in the other species ($|Z|=0.28$, 1.07 and 0.33, $N=15$, 14 and 22 for thin-billed prion, Antarctic prion and common diving-petrel, respectively, all $P>0.25$; Fig. 5). Flight calling was significantly reduced only in the blue petrel, in females (Fig. 5).

DISCUSSION

Responses of skuas to petrel calls

Brown skuas often responded to playbacks by approaching the calls of their main prey species. Brown skuas hunt at night, when petrels attend their breeding grounds, and usually wait and look for their prey on the ground (Furness 1987; Young et al. 1988). In the absence of light (on dark nights), vocalizations can thus provide skuas with information needed to locate and catch their prey. The probability of response depended strongly on the distance from the playback source, suggesting that skuas mainly approach calling petrels from close by.

Regrouping species into five prey categories, we found that the attractiveness of petrel calls to skuas was more-over tuned to the incidence of the species in their diet. The blue petrel was the main and preferred prey of brown skuas: the incidence of predation upon this species exceeded relative abundance on both study islands (Montcorps et al. 1998; Mougeot et al. 1998). Prions were skuas' secondary prey, and their incidence in the diet of skuas overall matched prey availability at colonies, whereas other prey species (diving-petrels and storm-petrels) were underrepresented in the diet of skuas. Our results showed that skuas approached significantly more frequently, and from a greater distance, to playback calls of blue petrel than those of prions, and the latter more than those of other prey categories (including diving-petrels, storm-petrels and controls). We also found that between-prey category differences in call attractive-ness were always greater than within-prey category differences. Petrel species within a given prey category were also close relatives (storm-petrels, diving-petrels and prions), and call similarity was thus overall higher within than between the prey categories (see also sonagrams in Fig. 1).

Our playback design did not allow us to investigate and, in particular, control for possible intraspecific differ-ences in call attractiveness to skuas. Since we mixed calls of different males on the same tape, observed differences in call attractiveness to skuas may result from a particu-larly attractive, or nonattractive, male call of a given species. We believe that such a 'tape effect' is an unlikely explanation for differences in attractiveness to skuas for the following reasons. First, within-prey category (which was the replicate in our statistical design) differences were never significant, in contrast to between-prey category differences. Second, intraspecific variations in petrel calls were minimal in our experimental design since all play-back calls of a given species were from Kerguelen and from the same sex (see Bretagnolle 1996 for a review of patterns of intraspecific call variations in petrels). Third, intraspecific call variation is much lower than inter-specific call variation, even for closely related species like prions (Bretagnolle et al. 1990). Therefore, we are confi-dent that the observed differences in playback call attrac-tiveness to skuas resulted from their interest in the species' call (following incidence in their diet). We thus suggest that petrel calls provide the information needed for skuas to locate (and catch) prey. Moreover, the fact that call attractiveness matched the incidence of the species in the diet of skuas, relative to their local abun-dance at colonies, also suggests that the use of petrel calls might be the mechanism of prey selection by skuas observed on both study islands (Montcorps et al. 1998; Mougeot et al. 1998).

Listening behaviour by skuas probably imposes a major constraint on petrel communication, particularly for the main prey species: advertising petrels face a trade-off between signalling (calling) and avoiding detection by predators. As emphasized above, vocalizations are the most suitable way for petrels to communicate in colonies, particularly in a sexual context (Bretagnolle 1996). Bio-metric comparison has revealed that the majority of blue

petrels and thin-billed prions killed by skuas are non-breeders, that is young birds not yet paired and engaged in reproduction (Mougeot & Bretagnolle, in press). These nonbreeders attend the breeding colonies to look for a burrow and to advertise for a mate (Storey 1984; Bretagnolle et al. 1998). In contrast, breeding birds benefit from the relative safety of burrows (although skuas sometimes excavate birds from their burrows), and are much less vocal in colonies (Storey 1984; James & Robertson 1985; Brooke 1990). In the majority of petrel species, courtship thus probably places males at greater predation risk: they first compete with other males for burrows and then vocalize from the ground to attract females that respond in flight (Bretagnolle 1990b, 1996; Bretagnolle et al. 1998). Skuas, hunting on the ground, are thus more likely to catch males, and especially those that are advertising themselves. Several petrel species perform some courtship in flight (for example in the genus *Pterodroma*, including the white-headed petrel, and, to a lesser extent, the genus *Pelecanoides*, including at least one of the species studied). This might be a way to reduce predation risk further (Bretagnolle 1996).

Predation Risk and Petrel Responses

Studies of antipredator behaviours typically focus on tactics such as vigilance, alarm calling and mobbing (see Lima & Dill 1990 for a review). Less information is usually available regarding the cues available to prey for detecting predators, or for evaluating variations in predation risk. Several studies, however, have indicated that some bird species are able, using auditory cues associated with the predator, to increase the probability of early detection and avoidance (Hauser & Wrangham 1990; Hauser & Caffrey 1994). Early detection and silence are common defences against listening predators, as described in insects (e.g. Spangler 1984; Belwood & Morris 1987) and amphibians (Ryan et al. 1981, 1982), and are the simplest ways of avoiding predators. Playbacks of brown skua calls to petrels showed that the blue petrel, the thin-billed and Antarctic prions, and the common diving-petrel were able to recognize the vocalizations of their main predator and responded by reducing their vocal activity. They distinguished the skua's calls from those of nonpredator species (controls). This was particularly true of birds on the ground, that is, those most at risk. In-flight calling was also reduced in response to playbacks of skua calls, but only in the blue petrel, suggesting that some flying females avoided the area where skua calls were played, or that the lower calling rate from males on the ground attracted fewer females or elicited less calling from females in flight. Individuals on the ground that stopped calling probably reduced their conspicuousness, and thus their predation risk. Only the main prey species, whose calls were the most attractive to skuas, reduced their vocal activity during playbacks of skuas.

The effects of predation on mating tactics have not received much consideration, although it is generally assumed that males incur higher predation risk than females, as a result of both intrasexual competition and advertising to females (Burk 1982; Ryan 1985; Magnhagen 1991; Berglund 1993; Andersson 1994; Acharya 1995; Fuller & Berglund 1996). In the blue petrel, the species suffering the highest predation rate, males (the riskier sex, as emphasized above) reduced their vocal activity significantly more than females during playbacks of predator calls. The results thus suggest that predator avoidance behaviour was tuned to predation risk, at species and sex levels. Mating behaviour may also vary with the level of predation risk (Fuller & Berglund 1996; Acharya & McNeil 1998). Predation risk is a likely reason why petrels (at least small species) are nocturnal on their breeding grounds (Bretagnolle 1990a; Brooke & Prince 1991; McNeil et al. 1993). Indeed, the majority of petrel species, and particularly nonbreeders, reduce their activity (attendance rate, vocal activity) in colonies on moonlit nights, probably in response to an increased predation risk (Watanuki 1986; Bretagnolle 1990a; McNeil et al. 1993). We have shown elsewhere that, on Mayes Island, skuas caught more prey, and particularly more blue petrels, on moonlit nights (Mougeot & Bretagnolle, in press). Vocal activity of brown skuas also increased on moonlit nights, probably because higher foraging effort resulted in more frequent territorial interactions between neighbouring pairs. As a consequence, vocal activity and colony attendance by nonbreeding petrels of the main prey species were drastically reduced on those nights. We have shown that these species could use skua calls for predator detection. Increased vocal activity of skuas on moonlit nights might thus be a relevant cue for these species to assess variation in predation risk, and reduce courtship activities accordingly.

In conclusion, our results suggest that brown skuas, during their nocturnal hunts, use petrel calls to locate and catch prey and also probably to select prey species. This predator thus acts as an illegitimate receiver of the petrels' communication, and probably imposes constraints on petrel courtship: petrel males vocalize from the ground to attract females, and thus face a trade-off between advertising themselves and avoiding predation by skuas. We also showed that the main prey species could use skua calls for predator detection, and stopped calling accordingly, reducing their conspicuousness and predation risk. Species subject to intense predation might also be expected to use signals with a physical structure that reduces detectability by predators (e.g. Brown 1982; Klump & Slater 1984; Ryan 1985; Bradbury & Vehrencamp 1998). Experiments should be conducted: (1) at the interspecific level, to define the characteristics of vocalizations that may explain between-species differences in vulnerability to skuas (in some petrel species, vocalizations are partly 'scrambled', which may help to reduce detectability and predation risk; Bretagnolle 1996); and (2) at the intraspecific level, to investigate whether some males have more detectable and locatable calls than others, hence a higher mating success as well as a higher predation risk, possibly leading to a handicap process.

Acknowledgments

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