



Neighbour–stranger discrimination in the little owl, *Athene noctua*

LOÏC A. HARDOUIN, PIERRE TABEL & VINCENT BRETAGNOLLE

Centre d'Etudes Biologiques de Chizé, CNRS UPR 1934, Villiers-en-Bois

(Received 8 January 2004; initial acceptance 3 February 2004;
final acceptance 7 September 2005; published online 12 June 2006; MS. number: 7949R)

Based on theoretical considerations, neighbour–stranger discrimination in territorial contexts is predicted and has been reported in many passerine birds. It has seldom been investigated in territorial nonpasserine species. We experimentally investigated neighbour–stranger discrimination in a year-round territorial nocturnal raptor, the little owl. We used playback of hoots to investigate whether territory owners discriminated neighbours from strangers when playback occurred at the usual location for the neighbour or at an unusual location. Male little owls responded significantly less to their neighbour's hoots played back from the usual location. However, responses to playback of a neighbour from an unusual location were similar to responses to playback of a stranger's hoots from either location. We conclude that little owls can discriminate between the hoots of neighbours and strangers. This study provides the first experimental evidence in owls for this level of neighbour–stranger discrimination, which is comparable to results found for passerines.

© 2006 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

There is an abundant literature on the adaptive value to birds of discrimination between individuals, especially with regard to relationships between parent and offspring (Medvin & Beecher 1986; Jones et al. 1987; Van Elsacker et al. 1988; Aubin & Jouventin 1998) and between mates (Beletsky 1982; Marzluff 1987; reviewed in Ratcliffe & Otter 1996). In birds, individual discrimination is achieved mainly through vocal cues (Emlen 1972; Falls 1982; Catchpole & Slater 1995; Bradbury & Vehrencamp 1998) and the necessary individual differences in calls or songs have been documented in many species (e.g. Emlen 1972; Horn & Falls 1996).

Many species of bird are territorial, excluding competitors by a combination of advertisement, threat and attack (Bradbury & Vehrencamp 1998), and benefiting from exclusive access to resources such as food, mates and nest sites (Davies & Houston 1984; Krebs & Davies 1987). However, territoriality can have important individual costs, such as time lost, energetic costs of signalling, patrolling and chasing, and risks of predation and injury, particularly when fighting is the outcome of the encounter (Bradbury & Vehrencamp 1998). Territorial animals may offset some of these costs by minimizing responses to neighbours, because neighbours may not necessarily constitute a serious threat to adjacent territory holders, at least when they

remain within their territories. This reduced aggressiveness towards neighbours has been referred to as the 'dear enemy' phenomenon (Fisher 1954) and has been developed within game theory modelling (Ydenberg et al. 1988; Getty 1989; Temeles 1994). Clearly, an ability to discriminate between neighbours and non-neighbours is necessary for reduced dear enemy responses to neighbours. Such discrimination has been less often studied in territorial contexts than similar abilities in mate and offspring relationships (Stoddard 1996), although its adaptive value has been emphasized repeatedly (e.g. McGregor & Falls 1984; McGregor 1993; McGregor & Dabelsteen 1996). The dear enemy phenomenon has received considerable experimental support in passerines, which benefit from territoriality through exclusive access to resources and which learn many aspects of vocalizations. Thus, we might expect them to be able to discriminate on the basis of vocal cues (Lambrechts & Dhondt 1995).

Neighbour–stranger discrimination has been far less studied in territorial nonpasserines with well-developed acoustic communication (exceptions include blue grouse, *Dendragapus obscurus*: Falls & McNicholl 1979; pukeko, *Porphyrio p. melanotus*: Clapperton 1987; petrels (families Procellariidae, Hydrobatidae and Pelacanoides): Bretagnolle 1996). Tawny owls, *Strix aluco*, respond differently to vocal signals (hoots) of neighbours and strangers played back at the boundary with the neighbour (the 'usual' location; Galeotti & Pavan 1993). This result shows that tawny owls can discriminate familiar hoots from unfamiliar

Correspondence: L. A. Hardouin, CNRS-CEBC, 79360 Villiers-en-Bois, France (email: hardouin@cebc.cnrs.fr).

hoots. However, a playback paradigm with four types of stimuli (neighbour versus stranger at usual and unusual locations) is usually considered necessary to demonstrate neighbour–stranger discrimination (e.g. Falls 1982), because this subset of familiar–unfamiliar discrimination tasks combines location and individual identity information to elicit the behavioural difference underlying the dear enemy effect.

In this study, we experimentally tested whether little owls can distinguish between a neighbour and a stranger. We used the established four-stimuli playback discrimination paradigm with two categories of hoots (neighbour hoots and stranger hoots), played from two locations (the usual boundary and the unusual boundary of the territory, i.e. the opposite side where no bird is usually present). Little owls are small nocturnal raptors that can occur at high local densities; their relatively long life (5–6 years) and high site fidelity to year-round territories (Juillard 1984; Exo 1992; Génot 2001) are factors likely to enhance strong vocal interactions between neighbours; therefore, we considered this species likely to benefit from the dear enemy phenomenon.

METHODS

Study Species and Area

The little owl (family Strigidae) is a territorial, resident, philopatric and monogamous nocturnal raptor (Exo 1992; Génot 1992a; Génot et al. 1997), usually inhabiting open fields (Van Nieuwenhuysse & Bekaert 2001; Perrus et al. 2002). Up to 22 types of vocalizations have been described, varying according to sex, age and context (Exo & Scherzinger 1989), but two call types predominate: the male hoot and the chewing call (Exo 1984; Exo & Scherzinger 1989; personal observation). The male hoot is usually produced in strophes over the entire breeding season, although vocal activity peaks in March (Génot 1992b, 2001). Females occasionally utter hoots, but these are harsher and louder than male hoots and are uttered singly (Exo & Scherzinger 1989; personal observation). Furthermore, lone females never spontaneously produce hoots. Both chewing calls and hoots are used by males in territorial contests and in response to playback. However, in spring, the hoot is predominantly used (>90% of responses to playback in our study), although territorial responses that begin with hoots may sometimes finish with chewing calls. We thus focused on male hoots because males use them to defend their territories (Schönn et al. 1991). Hoots vary between male little owls but show little intraindividual variation over time (Fig. 1). We were able to discriminate 300 spectrograms from 12 individual males with a success rate of 94% using discriminant analyses based on four frequency and four temporal parameters (L. A. Hardouin & V. Bretagnolle, unpublished data).

We conducted fieldwork from 2 April to 22 May 2002 and from 27 April to 19 May 2004 in a 350-km² agricultural plain in western France (46°14'N, 00°24'W, WGS84), which is dominated by a system of intensive cereals, oil-seed rape and spring-sown crops (maize,

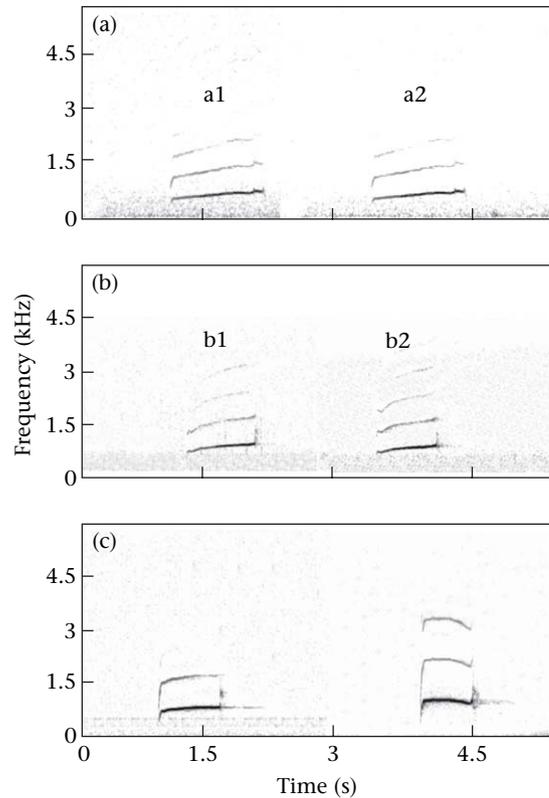


Figure 1. Comparison of hoot spectrograms from four different male little owls. (a, b) Hoots from males that were tape recorded twice the same year (hoots termed a1/a2 and b1/b2, respectively). (c) Hoots from two males that were tape recorded at the same location but two different years.

sunflower and pea). No trees or fragmented forests occur in this farmland, and little owls are restricted to villages, where they can find nest cavities. The density of little owls in our study area averaged 0.49 pairs/km² but locally reach 1.53/km² (Bretagnolle et al. 2001).

General Experimental Design

To test whether little owls are able to discriminate between conspecifics, we played back a hoot to a territorial owner. The experimental design included two categories of hoots in two locations (Fig. 2), resulting in four treatments (1) neighbour hoots (i.e. a familiar individual with which the tested male shared a territory boundary); (2) stranger hoots (an unfamiliar individual with which the tested male had never interacted recorded several kilometres from the subject, often in a different year); (3) playback at the usual location; and (4) playback at the unusual location (i.e. the opposite side of the territory where no bird was usually present; e.g. Falls & Brooks 1975). As explained earlier, studies with passerines have shown that playback from the usual location elicits less reaction to the neighbour stimulus than to the stranger stimulus, and the neighbour stimulus from the unusual location elicits as strong a reaction as does the stranger stimulus from either location (Ydenberg et al. 1988).

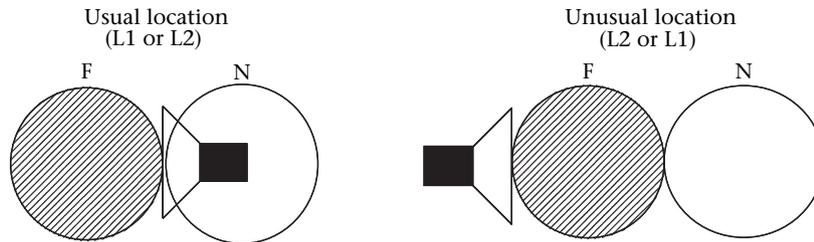


Figure 2. Description of the experimental design. F is the subject (shaded circle), and N is its neighbour (open circle). The loudspeaker was placed alternately on the midpoint between the subject and its neighbour (usual location) or on the opposite side (unusual location). Location order (L1 or L2) was randomly determined. See [Methods](#) for further details.

Typically, little owls use the same perching site to hoot (personal observation), allowing us to be confident of the placing of the playback loudspeaker. For playback from the usual location, we placed the loudspeaker at the midpoint between the hooting sites of the subject and its neighbour (on average 50 m between subject and loudspeaker, range 40–60 m). The hooting sites of little owls are spatially regular, so we chose as the unusual location for the loudspeaker the opposite location (i.e. at 180° and at the same distance from the subject).

Playback Methodology

We studied seven little owls in 2002 and 14 in 2004. Each had a neighbour about 100 m distant. We recorded the vocalizations of the 21 subjects and their respective neighbours before the experiment. For this, we elicited calling behaviour with playback (using hoots from non-neighbours that were not used in the experiment) and recorded the vocalizations with a Sennheiser MKH-815T directional microphone, connected to a Sony TC-D5M tape recorder. The recordings were always made close to owls (10–50 m), from 2000 to 0400 hours in good recording conditions (e.g. on windless nights). There was no consistent pattern in the distance at which playback stimuli were recorded in relation to stimulus category, so distance was not a source of bias in our results.

In 2004, two males were located less than 200 m from males used as subjects in 2002; however, inspection of spectrograms indicated that these males were different individuals. Stranger hoots were recorded ($N = 5$ in 2002, 14 in 2004) at different sites and in previous years and we carefully selected them to have comparable recording quality. Thus, we limited the potential influences of pseudoreplication (Kroodsmma 1989) and execution errors (McGregor et al. 1992). We did not use neighbours as subjects, that is, this was not a reciprocal design.

To prepare playback tapes we used Cooledit 3.0 trial version software (Syntrillium, Phoenix, AZ, U.S.A.) and Audacity freeware (D. M. Mazzoni, <http://audacity.sourceforge.net>) to reduce background noise and homogenize each recording. Hoots were played back in the field from a Sony WM-EX12 cassette player connected to a Barthe Eduvoice Plus loudspeaker (23 W efficient power, frequency response 50–6000 Hz \pm 3 dB) that was pointed towards the subject. All playbacks were played at the same

volume as estimated by ear, approximating the loudness of a real hoot.

We conducted 42 tests (each test encompassed all four treatments), where each of the 21 males was tested twice (we use the term ‘round’ to refer to this repetition) to take into account the intraindividual variation of the territorial response.

The two locations (the usual, U, and the unusual, Un, locations) and the two hoot types (the neighbour, N, and the stranger, S) provided four combinations of treatments. Each test consisted of these four successive treatments (Fig. 2): location 1 (playback 1 (P1), silent period 1 (SP1)); location 1 (playback 2 (P2), silent period 2 (SP2)); location 2 (P1, SP1); location 2 (P2, SP2). The location order and the successive playback presentations for each location were randomly chosen in each test. Thus, if location 1 was the usual location, then location 2 was the unusual location, and vice versa. Similarly, if P1 was stranger hoots, then P2 was neighbour hoots, and vice versa. Each silent period was used for recording behaviour of the subjects and lasted 5 min. To move the speaker between the two locations (about 100 m apart) during an experiment, we used a car, disturbing the subject to a similar degree to the usual road traffic.

All playbacks contained 10 hoots and lasted 38–67 s (neighbours: $\bar{X} \pm \text{SD} = 53.1 \pm 7.3$ s; strangers: 53.6 ± 5.3 s; paired t test: $t_{34} = -0.13$, $P = 0.89$). Silences between hoots in playbacks (4.32 ± 0.74 s) were also similar to natural interhoot silences (4.02 ± 1.13 s; $t_{31} = -0.95$, $P = 0.34$; unpublished data). Playback began only after the subject was silent for 2 min. We also required a minimum interval of 2 min without calling between each treatment (range 2–20 min) to allow recovery of the subjects. Therefore, a complete test lasted at least 24 min (at least 20 min of silence and four playbacks lasting, on average, 54 s each). Playback experiments were conducted at any time from dusk to dawn, as the probability of response did not decrease during the night (unpublished data). Seven subjects did not respond to two or more treatments (five did not respond to any, two others responded only to the last treatment). We could not be sure that these males were present during playback (they could have been hunting), so we excluded these seven tests from the analyses. We repeated the tests at least 2 days afterwards on the same individuals; they all responded during this second test, where they received the same neighbour hoots and different stranger hoots.

Response Measures and Statistical Analysis

We quantified the vocal response to playback and also measured the degree of agonistic behaviour during response as follows: latency (time elapsed before first vocal response), length of response, hoot rate (number of hoots/min) and number of flights. The 'many-measures' approach (in our case, four) is potentially flawed as the measures are likely to be correlated (McGregor 1992), so we performed a principal components analysis (PCA) on the four response variables. The first axis accounted for 52.4% of variance (Table 1), and all original variables were correlated with the first principal component (all >0.40 ; Table 1). We thus used the scores of the first principal component of the PCA to perform statistical analyses on the degree of agonistic response.

We used logistic regression (with mixed-effects approach) when analysing response ratio (under a binomial distribution), and generalized linear mixed-effect models (GLMM) for PC1. The fixed factors of the model were playback treatment (neighbour versus stranger, in two locations), playback order (from the first to the fourth treatment on each subject), effect of the repeated playback (interaction between order and treatment, i.e. the effect of treatment order in each repeated measures test), year and the effect of the neighbour's response (whether or not the neighbour responded to the playback) on the subject (interaction between treatment and neighbour's response, used only in the GLMM). Round (i.e. the two replicated tests for each subject) was nested within subjects, and these were treated as random variables in the model. Random variables are distinguished in that we were interested not in their parameter values, but only in the variance that they explained (see Results, Table 3). These models are particularly useful when the experimental design involves both temporal pseudoreplication, that is, repeated measures taken from the same individual, and spatial pseudoreplication (e.g. nested designs; Crawley 2002). PC1 scores were not normally distributed (Kolmogorov-Smirnov test: $D = 0.208$, $N = 168$, $P = 0.001$) and therefore we checked visually that the residuals of the model showed no trends and were not correlated with fitted values.

Table 1. Results of the principal components analysis performed on the four response parameters of little owls

	Component			
	1	2	3	4
Eigenvalues	1.44	0.97	0.86	0.47
Percentage of variance	52.4	23.7	18.9	5.0
Cumulative percentage	52.4	76.1	95.0	100
Measures of response*				
Latency	0.91	-0.22	0.02	-0.33
Length of response	-0.79	0.38	0.40	-0.25
Hoot rate	-0.68	-0.25	-0.66	-0.15
Number of flights	-0.40	-0.83	0.38	0.01

*Matrix of correlation between response variables and principal components. See Methods for further details.

We started with the global model (i.e. all explanatory variables and their interactions) and compared it with submodels, from which we sequentially deleted nonsignificant terms until we ended up with the minimal model. For the model selection procedure we used the parsimony principle, based on the Akaike's information criterion (AIC): the lower the AIC value, the more parsimonious the model. We considered two models to be significantly different when the difference between their AICs was greater than 2 (Burnham & Anderson 2002). For testing hypotheses on the fixed effects, we used an estimation method set to the maximum likelihood rather than the restricted maximum likelihood to ensure that the test compared likelihoods based on the same data (Venables & Ripley 2002). We used the freeware R 1.7.1 (Ihaka & Gentleman 1996) for all statistical analyses.

RESULTS

Effect of Treatment on Playback Response Ratio

Overall, the response ratio to playback was high: 94.6% and 88.4% of responses were obtained in 2002 and 2004, respectively, for all treatments ($N = 168$ treatments, i.e. four treatments repeated for 42 tests, on 21 different individuals). Treatment was the most important factor. The most parsimonious model had treatment as a single fixed factor (random factors: subjects (intercept) = 0.128, round in subject (intercept) = 0.08, residuals = 0.99). There was no significant effect of repeated playback (i.e. repeated measures); treatment \times order: $F_{9,108} = 0.09$, $P = 0.99$, or of playback order ($F_{3,117} = 0.18$, $P = 0.90$), so a playback did not influence the response ratio in the following playback. Therefore, we found no evidence of a reaction threshold (found in some passerine species, Falls & D'Agincourt 1981). The response ratio did not differ significantly between years ($F_{1,19} = 1.23$, $P = 0.28$) and there was no significant interaction between year and treatment ($F_{3,120} = 0.34$, $P = 0.79$). The response ratio was, however, significantly altered by the playback treatment ($F_{3,123} = 4.96$, $P = 0.002$): little owls responded significantly less to the neighbour in the usual location (73.8% of responses) than to the other three treatments ($>95\%$ of responses in all cases).

Effect of Treatment on Response Intensity

The four response measures consistently showed lowest responses to neighbour hoots from the usual location (Fig. 3), and the same is true for the single measure of response, PC1, obtained through the PCA (Fig. 4). The most parsimonious model had treatment, year and neighbour's response as factors (Tables 2, 3). The intensity of territorial response (PC1) was significantly affected by treatment (Table 2), but was not affected by either the order of playback ($F_{3,116} = 0.21$, $N = 168$, $P = 0.88$) or the repeated term (treatment \times order effect: $F_{9,107} = 1.08$, $P = 0.37$), suggesting that there was no effect of repeated playback. A slight difference in territorial response appeared between years

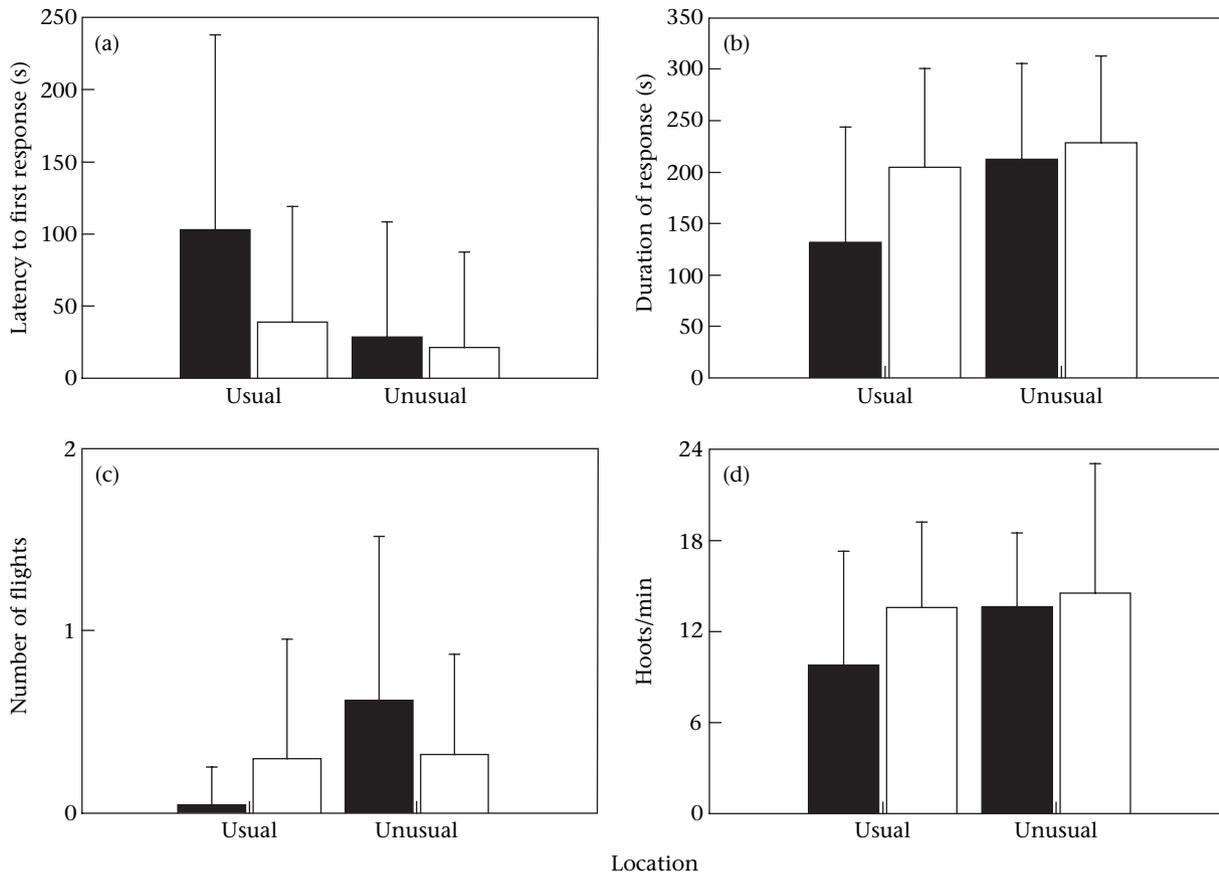


Figure 3. Means + SD of the four response parameters of male little owls after playback of neighbour (■) or stranger (□) hoots in usual and unusual locations between territories.

(Table 2), but there was no interaction between year and treatment ($F_{3,119} = 0.95$, $P = 0.41$). Males reacted significantly more to stranger hoots from the usual location than to neighbour hoots (Fig. 4, Table 3). They were strongly influenced by the location of the playback of neighbour hoots (Fig. 4, Table 3). We found no significant difference between responses to neighbour or stranger hoots from the unusual location (treatment Un/N versus Un/S; paired t test: $t_{122} = -0.47$, $P = 0.63$; Table 3, Fig. 4). Finally, although neighbours often responded to the playback, they did not influence the response of the subject (Table 2) regardless of the treatment (treatment \times neighbour's response: $F_{3,104} = 1.00$, $P = 0.39$).

DISCUSSION

Vocal individuality has been documented in at least 136 species of birds (Stoddard 1996). Most territorial signals studied have revealed individual discrimination capabilities, which require a sufficiently complex signal within parameter space for individual variation, and a brain that can integrate these variants (Bradbury & Vehrencamp 1998). Individual differences in calls or songs can be coded in temporal aspects, fundamental frequency and harmonic structure (Weary 1989, 1996), and have been related to individual discrimination in passerines (reviewed

in Lambrechts & Dhondt 1995) and nonpasserines, particularly seabirds (e.g. Bretagnolle 1996).

Hoots are used by male owls in territory settlement (defence against competitors or rivals) and mate attraction (Ritchison et al. 1988; Ganey 1990), whereas other calls are used by males and females for defence against predators (McKell Sproat & Ritchison 1994). Thus the use of vocalizations in owls appears to be comparable to that reported for most passerines (Catchpole & Slater 1995). Individual differences in owl hoots have been reported (e.g. tawny owl: Galeotti & Pavan 1991; saw-whet owl, *Aegolius acadicus*: Otter 1996), but the discrimination ability of these birds has been investigated only once (Galeotti & Pavan 1993). Tawny owls distinguished between familiar and unfamiliar hoots: both males and females increased their hooting frequency and decreased the latency to hoots in response to unfamiliar tawny owls (Galeotti & Pavan 1993). However, our study is the first experimental demonstration that owls are able to discriminate a subset of familiar and unfamiliar hoots that is important in territory defence, that is, hoots of neighbours versus strangers. We found that male response to a neighbour's hoots from that neighbour's usual location was significantly lower than to a stranger's hoots from the same location. Males also responded equally strongly to hoots from both neighbours and strangers from an unusual location. We conclude that little owls have developed the ability to

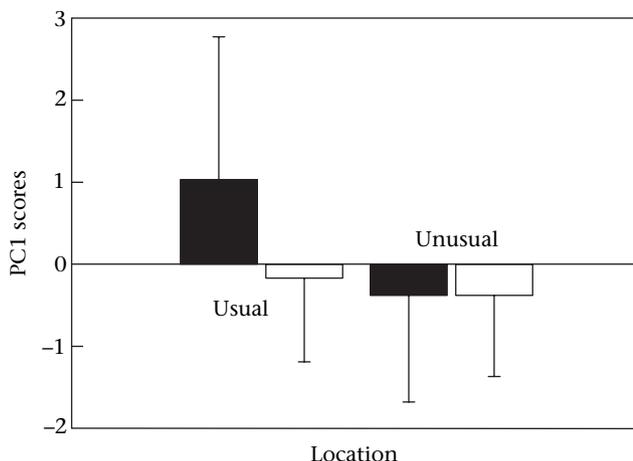


Figure 4. PC1 scores of the principal components analysis made on the four response parameters according to the hoot playback in two locations (usual or unusual): neighbour (■) or stranger (□).

discriminate between the hoots of neighbour and stranger males, in accordance with theoretical predictions (Ydenberg et al. 1988) of the dear enemy hypothesis.

In all studies that have used the same playback paradigm that we used, the unusual location (sometimes termed the opposite boundary, Stoddard 1996) for playback has necessarily been arbitrarily determined. Therefore, we cannot exclude the possibility that the loudspeaker was actually within the focal bird's territory. However, in the white-throated sparrow, *Zonotrichia albicollis* (Falls & Brooks 1975), and the song sparrow, *Melospiza melodia* (Stoddard et al. 1991), playback elicited more similar responses from the unusual location and centre of the territory than either compared to usual locations. This result suggests that variation in the exact position of the unusual location would not produce qualitatively different conclusions.

Thus, neighbour–stranger discrimination is an economic system of territory defence that potentially saves physiological costs by minimizing the energy expended on aggressive acts, prevents escalated contests between neighbours, and decreases time lost and predation risk. The sedentary nature and site fidelity of little owls enhance the potential selective advantage by minimizing costs of territoriality in high-density local populations with a stable social composition. Discrimination capacity could develop with increasing population density and with experience, as Phillimore et al. (2003) suggested for chickadees, *Poecile atricapillus*.

Bee & Gerhardt (2001) pointed out that a territorial animal could be habituated to an individually distinct property of a communication signal, and to the location from

Table 2. ANOVA results of the linear mixed-effects model with *df*, *F* values, and *P* values for Wald tests for the terms in the model

	<i>df</i>	<i>F</i>	<i>P</i>
Treatment	3,122	12.8	<0.0001
Year	1,19	3.6	0.07
Response of neighbour	1,122	2.5	0.11

Table 3. Results of the linear mixed-effects model fitted by maximum likelihood, with parameter estimate (i.e. fixed-effects estimates), approximate standard error, denominator degrees of freedom, ratios between the estimates and their standard errors (*t* value) and *P* value from a *t* distribution for the fixed-effects table

Fixed effects	Estimate	SE	<i>df</i>	<i>t</i>	<i>P</i>
Treatment U/S versus U/N	-1.13	0.27	122	-4.05	0.0001
Treatment Un/N versus U/N	-1.45	0.27	122	-5.22	<0.0001
Treatment Un/S versus U/N	-1.58	0.28	122	-5.67	<0.0001
Year (2004 versus 2002)	0.44	0.24	19	1.78	0.09
NR(0) versus NR(1)	-0.33	0.21	122	-1.58	0.11
Random effects	Intercept	Residual			
Subjects		0.27			
Round in subjects		0.06		1.25	

For random effects, the estimate of the residual standard deviation and the standard deviation of the random effects (intercept) are provided. U: usual location; Un: unusual location; S: stranger hoot presentation; N: neighbour hoot presentation; NR(0): neighbour did not respond; NR(1): neighbour responded.

which the signal originates. Our paradigm could not separate between individual familiarity and individual identity because we did not specifically test individual discrimination, and therefore it is not currently possible to identify which factor elicited the differential response we observed (i.e. individual identity versus location). It would be interesting to test whether little owls can discriminate between neighbours by using a neighbour/neighbour paradigm (playback stimuli of same familiarity level and where the locations are balanced; Stoddard 1996).

To conclude, our study provides the first indirect evidence of learning capacity in a territorial context for an owl. Neighbour–stranger discrimination is well established in passerines (Lambrechts & Dhondt 1995), which learn their calls and songs, and therefore have the cognitive capacities to learn signal properties allowing individual discrimination. Wiley (2005) suggested that associative learning (instead of, or in addition to, habituation) could be involved in this level of discrimination. Appleby & Redpath (1997) suggested that, unlike passerines, owls apparently do not learn their hoots. Hence, the evidence that we provide here for neighbour–stranger discrimination in an owl suggests that at least some nonpasserines also have the ability to detect, memorize and learn particular acoustic details in hoots, which may be furthered by large individual differences in hoots (Wiley 2005). We suggest that little owls developed this ability in response to the constraints of nocturnal behaviour combined with strong territorial behaviour caused by high levels of competition for nest sites, which appear to limit population size in this species (Van Nieuwenhuysse et al. 2001).

Acknowledgments

We thank Gwénaél Beauplet, David J. Carslake, Thomas de Cornulier, Véronique Gosson, Pablo Inchausti, Alexandre

Millon, Lesley M. Montemayor and David Reby for their contributions at various stages of our work, Dr Dan Wright, Department of Psychology, University of Sussex, whose explanations helped to clarify our statistics, and Paolo Galeotti, Peter McGregor, Marc Naguib and the anonymous referees for their constructive comments and suggestions on the manuscript. L.A.H. received a Ph.D. grant from Louis Pasteur University, Strasbourg, France.

References

- Appleby, B. M. & Redpath, S. M.** 1997. Variation in the male territorial hoot of the tawny owl *Strix aluco* in three English populations. *Ibis*, **139**, 152–158.
- Aubin, T. & Jouventin, P.** 1998. Cocktail-party effect in king penguin colonies. *Proceedings of The Royal Society of London, Series B*, **265**, 1665–1673.
- Bee, M. A. & Gerhardt, H. C.** 2001. Neighbour–stranger discrimination by territorial male bullfrogs, *Rana catesbeiana*: II. Perceptual basis. *Animal Behaviour*, **62**, 1141–1150.
- Beletsky, L. D.** 1982. Vocal mate recognition in male red-winged blackbirds, *Agelaius phoeniceus*. *Behaviour*, **84**, 124–134.
- Bradbury, J. W. & Vehrencamp, S. L.** 1998. *Principles of Animal Communication*. Cambridge, Massachusetts: Sinauer.
- Bretagnolle, V.** 1996. Acoustic communication in a group of nonpasserine birds, the petrels. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 160–177. Ithaca, New York: Cornell University Press.
- Bretagnolle, V., Bavoux, C., Burneleau, G. & Van Nieuwenhuysse, D.** 2001. Abundance et distribution des chevêches d'Athéna: approche méthodologique pour des enquêtes à grande échelle en plaine céréalière. *Ciconia*, **25**, 173–184.
- Burnham, K. D. & Anderson, D. R.** 2002. *Model Selection and Multi-Model Inference: a Practical Information-Theoretic Approach*. 2nd edn. New York: Springer-Verlag.
- Catchpole, C. K. & Slater, P. J. B.** 1995. *Bird Song: Biological Themes and Variations*. Cambridge: Cambridge University Press.
- Clapperton, B. K.** 1987. Individual recognition by voice in the pukeko, *Porphyrio porphyrio melanotus* (Aves: Rallidae). *New Zealand Journal of Zoology*, **14**, 11–18.
- Crawley, M. J.** 2002. *Statistical Computing: An Introduction to Data Analysis using S-plus*. New York: J. Wiley.
- Davies, N. B. & Houston, A. I.** 1984. Territory economics. In: *Behavioural Ecology. An Evolutionary Approach*, 2nd edn. (Ed. by J. R. Krebs & N. B. Davies), pp. 148–169. Oxford: Blackwell Scientific.
- Emlen, S. T.** 1972. An experimental analysis of the parameters of bird song eliciting species recognition. *Behaviour*, **41**, 130–171.
- Exo, K. M.** 1984. Die akustische Unterscheidung von Steinkauzmännchen und -weibchen (*Athene noctua*). *Journal of Ornithology*, **125**, 94–97.
- Exo, K. M.** 1992. Population ecology of little owls *Athene noctua* in central Europe: a review. In: *The Ecology and Conservation of European Owls* (Ed. by C. A. Galbraith, I. R. Taylor & S. Percival), pp. 64–75. Peterborough: Joint Nature Conservation Committee.
- Exo, K. M. & Scherzinger, W.** 1989. Voice and inventory of call-notes of the little owl (*Athene noctua*): description, context and habitat adaptation. *Ecology of Birds*, **11**, 149–187.
- Falls, J. B.** 1982. Individual recognition by sounds in birds. In: *Acoustic Communication in Birds*. Vol. 2 (Ed. by D. E. Kroodsma & E. H. Miller), pp. 237–278. New York: Academic Press.
- Falls, J. B. & Brooks, R. J.** 1975. Individual recognition by song in white-throated sparrows. II. Effects of location. *Canadian Journal of Zoology*, **53**, 1412–1420.
- Falls, J. B. & D'Agincourt, L. G.** 1981. A comparison of neighbor–stranger discrimination in eastern and western meadowlarks. *Canadian Journal of Zoology*, **59**, 2380–2385.
- Falls, J. B. & McNicholl, M. K.** 1979. Neighbor–stranger discrimination by song in male blue grouse. *Canadian Journal of Zoology*, **57**, 457–462.
- Fisher, J.** 1954. Evolution and bird sociality. In: *Evolution as a Process* (Ed. by J. Huxley, A. C. Hardy & E. B. Ford), pp. 71–83. London: Allen & Unwin.
- Ganey, J. L.** 1990. Calling behaviour of spotted owls in Northern Arizona. *Condor*, **92**, 485–490.
- Galeotti, P. & Pavan, G.** 1991. Individual recognition of male tawny owls (*Strix aluco*) using spectrograms of their territorial calls. *Ethology, Ecology and Evolution*, **3**, 113–126.
- Galeotti, P. & Pavan, G.** 1993. Differential responses of territorial tawny owls *Strix aluco* to the hooting of neighbours and strangers. *Ibis*, **135**, 300–304.
- Génot, J.-C.** 1992a. Biologie de reproduction de la chouette chevêche *Athene noctua* scop., en bordure des Vosges du nord. *Ciconia*, **16**, 1–18.
- Génot, J.-C.** 1992b. Contribution à l'écologie de la chouette chevêche, *Athene noctua* (scop.) en France. Ph.D. thesis, Université de Dijon.
- Génot, J.-C.** 2001. Etat des connaissances sur la chevêche d'Athéna, *Athene noctua*, en bordure des Vosges du nord de 1984 à 2000. *Ciconia*, **25**, 109–118.
- Génot, J.-C., Juillard, M. & Van Nieuwenhuysse, D.** 1997. Little owl, *Athene noctua*. In: *The EBC Atlas of European Breeding Birds: Their Distribution and Abundance* (Ed. by W. J. M. Hagemeijer & M. J. Blair), pp. 408–409. London: T. & A.D. Poyser.
- Getty, T.** 1989. Are dear enemies in a war of attrition? *Animal Behaviour*, **37**, 337–339.
- Horn, A. G. & Falls, J. B.** 1996. Categorization and the design of signals: the case of song repertoires. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 121–134. Ithaca, New York: Cornell University Press.
- Ihaka, R. & Gentleman, R.** 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.
- Jones, I. L., Falls, J. B. & Gaston, A. J.** 1987. Vocal recognition between parents and young of ancient murrelets, *Synthliboramphus antiquus* (Aves: Alcidae). *Animal Behaviour*, **35**, 1405–1415.
- Juillard, M.** 1984. Eco-éthologie de la chouette chevêche, *Athene noctua* (scop.), en Suisse. Ph.D. thesis, Université de Neuchâtel.
- Krebs, J. R. & Davies, N. B.** 1987. Competing for resources. In: *An Introduction to Behavioural Ecology*, 2nd edn. (Ed. by J. R. Krebs & N. B. Davies), pp. 93–110. Oxford: Blackwell Scientific.
- Kroodsma, D. E.** 1989. Suggested experimental design for song playbacks. *Animal Behaviour*, **37**, 600–609.
- Lambrechts, M. M. & Dhondt, A. A.** 1995. Individual voice discrimination in birds. In: *Current Ornithology*. Vol. 12 (Ed. by D. M. Power), pp. 115–139. New York: Plenum.
- McGregor, P. K.** 1992. Quantifying responses to playback: one, many, or composite multivariate measures? In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 79–95. New York: Plenum.
- McGregor, P. K.** 1993. Signalling in territorial systems: a context for individual identification, ranging and eavesdropping. *Philosophical Transactions of the Royal Society of London, Series B*, **340**, 237–243.
- McGregor, P. K. & Dabelsteen, T.** 1996. Communication networks. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 409–425. Ithaca, New York: Cornell University Press.

- McGregor, P. K. & Falls, J. B. 1984. The response of western meadowlarks (*Sturnella neglecta*) to the playback of undegraded songs. *Canadian Journal of Zoology*, **62**, 2125–2128.
- McGregor, P. K., Catchpole, C. K., Dabelsteen, T., Falls, J. B., Fusani, L., Gerhardt, H. C., Gilbert, F. S., Horn, A. G., Klump, G. M., Kroodsma, D. E., Lambrechts, M. M., McComb, K. E., Nelson, D. A., Pepperberg, I. M., Ratcliffe, L. M., Searcy, W. A. & Weary, D. M. 1992. Design and interpretation of playback: the Thornbridge Hall NATO ARW consensus. In: *Playback and Studies of Animal Communication* (Ed. by P. K. McGregor), pp. 1–9. New York: Plenum.
- McKell Sproat, T. & Ritchison, G. 1994. The antipredator vocalizations of adult eastern screech-owls. *Journal of Raptor Research*, **28**, 93–99.
- Marzluff, J. M. 1987. Vocal recognition of mates by breeding piñon jays, *Gymnorhinus cyanocephalus*. *Animal Behaviour*, **30**, 62–74.
- Medvin, M. B. & Beecher, M. D. 1986. Parent–offspring recognition in the barn swallow (*Hirundo rustica*). *Animal Behaviour*, **34**, 1627–1639.
- Otter, K. 1996. Individual variation in the advertising call of male northern saw-whet owls. *Journal of Field Ornithology*, **67**, 398–405.
- Perrus, L., Génot, J.-C., Topin, F., Baudry, J. & Giraudoux, P. 2002. Répartition de la chevêche d'athéna (*Athene noctua scop.*) et variation d'échelle d'analyses des paysages. *Revue d'Ecologie (Terre Vie)*, **57**, 39–51.
- Phillmore, L. S., Sturdy, C. B. & Weisman, R. G. 2003. Does reduced social contact affect discrimination of distance cues and individual vocalizations? *Animal Behaviour*, **65**, 911–922.
- Ratcliffe, L. & Otter, K. 1996. Sex differences in song recognition. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 339–355. Ithaca, New York: Cornell University Press.
- Ritchison, G., Cavanagh, P. M., Belthoff, J. R. & Sparks, E. J. 1988. The singing behavior of eastern screech-owls: seasonal timing and response to playback of conspecifics songs. *Condor*, **90**, 648–652.
- Schönn, S., Scherzinger, W., Exo, K.-M. & Ille, R. 1991. *Der Steinkauz*. Leipzig: Urania Verlagsgesellschaft MBH.
- Stoddard, P. K. 1996. Vocal recognition of neighbors by territorial passerines. In: *Ecology and Evolution of Acoustic Communication in Birds* (Ed. by D. E. Kroodsma & E. H. Miller), pp. 356–373. Ithaca, New York: Cornell University Press.
- Stoddard, P. K., Beecher, M. D., Horning, C. L. & Campbell, S. E. 1991. Recognition of individual neighbour by song in the song sparrow, a bird with song repertoires. *Behavioral Ecology and Sociobiology*, **29**, 211–215.
- Temeles, E. J. 1994. The role of neighbours in territorial systems: when are they 'dear enemies'? *Animal Behaviour*, **47**, 339–350.
- Van Elsacker, L., Pinxten, R. & Verheyen, R. F. 1988. Timing of offspring recognition in adult starlings. *Behaviour*, **107**, 122–130.
- Van Nieuwenhuyse, D. & Bekaert, M. 2001. Modèle de régression logistique de prédiction de la qualité d'habitat de la chevêche d'athéna (*Athene noctua*) à Herzele, Flandre orientale (nord-est de la Belgique). *Ciconia*, **25**, 95–102.
- Van Nieuwenhuyse, D., Leysen, M., De Leenheer, I. & Bracquené, J. 2001. Towards a conservation strategy for little owl *Athene noctua* in Vlaanderen. *Oriolus*, **67**, 12–21.
- Venables, W. N. & Ripley, B. D. 2002. *Modern Applied Statistics with S*. 2nd edn. New York: Springer-Verlag.
- Weary, D. M. 1989. Categorical perception of bird song: how do great tits (*Parus major*) perceive temporal variation in their song? *Journal of Comparative Psychology*, **103**, 320–325.
- Weary, D. M. 1996. How birds use frequency to recognize their song. In: *Neuroethological Studies of Cognitive and Perceptual Processes* (Ed. by C. F. Moss & S. Shettleworth), pp. 138–157. Boulder, Colorado: Westview Press.
- Wiley, R. H. 2005. Individuality in songs of Acadian flycatchers and recognition of neighbours. *Animal Behaviour*, **70**, 237–247.
- Ydenberg, R. C., Giraldeau, L. A. & Falls, J. B. 1988. Neighbours, strangers, and the asymmetric war of attribution. *Animal Behaviour*, **36**, 343–347.