Ibis (2006), **148**, 664–671

Potential prey make excellent ornithologists: adaptive, flexible responses towards avian predation threat by Arabian Babblers *Turdoides squamiceps* living at a migratory hotspot

PIM EDELAAR[1,2]* & JONATHAN WRIGHT[3]
[1] *Royal Netherlands Institute for Sea Research, 1790 AB Den Burg, The Netherlands*
[2] *Department of Ecology & Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA*
[3] *Institute of Biology, Norwegian University of Science and Technology, Trondheim N-7491, Norway*

During spring raptor migration, resident, group-living, Arabian Babblers *Turdoides squamiceps* in Israel are exposed to many avian predators that differ in the level of predation threat that they pose. Accurate information about immediate safety while foraging may be provided by the sentinel, a high-perched non-foraging Babbler that actively scans and warns for predators. We tested whether, at this migratory hotspot, the bewildering number and diversity of potential avian predators (perhaps more than anywhere else in the world) may be more than a reliable sentinel could handle. We monitored ten Babbler groups regularly for a number of hours per day throughout the migration season, and scored whether the Babblers gave alarm calls when different bird species were in sight. Analyses showed that Babblers are very skilled in distinguishing between species of high and low predation threat (interspecific threat-sensitivity). In addition, Babblers distinguished accurately between encounters with dangerous vs. harmless individuals from predator species of potentially high predation threat (intraspecific threat-sensitivity). Overall, Babblers cautiously overestimated predation threat, probably because errors involving alarms for harmless predators have a lower fitness cost than errors involving attacks by dangerous predators that are ignored. However, fewer warnings were given for the more common predators of lower threat, which suggests that Babblers initially overestimated the risk of predation, but subsequently learned to assess the level of threat more accurately as soon as more information was available. Overall, our findings agree closely with theoretical predictions regarding adaptive and sophisticated anti-predation behaviour in a variable world.

From the point of view of an individual prey animal, predation events are rare and largely stochastic, but have a major impact on lifetime reproductive success. As a consequence, birds are expected to monitor the environment and track changes in the risk of predation (hereafter we use the term 'threat' for 'risk of predation', to avoid confusion with 'risk-sensitivity', cf. Vasquez & Kacelnik 1998). Because time available for various fitness-enhancing behaviours is often limited, potentially distracting behaviours such as foraging, territory defence and mating should be performed during periods of low predation threat, whereas a greater proportion of predator avoidance behaviours should be performed during periods with high threat (Lima & Bednekoff 1999). Such adjustments in behavioural time budgets assume that predation threat can be assessed correctly: that potential predators can be discriminated from non-predators (interspecific threat-sensitivity), and that their frequency in the local environment can be estimated accurately. Further adaptation to predator- or context-specific variation in threat is possible if prey species are sensitive to the levels of threat posed by each potential predator, depending on the specific circumstances of an encounter (intraspecific threat-sensitivity: Helfman 1989, Cavanagh & Griffin 1993). Relatively few studies on birds have tested for such flexibility in

*Corresponding author.
Email: w.m.c.edelaar@umail.leidenuniv.nl

sensitivity to predation threat other than distance to a potential predator (e.g. Cresswell 1993, Albrecht & Klvana 2004, Blumstein *et al.* 2004, Sordahl 2004, Kleindorfer *et al.* 2005, and references therein).

In birds, there is mixed evidence for the developmental basis of responses to predators. In some cases, innate responses have been found for the appropriate discrimination of predators or heterospecific mobbing calls (e.g. Veen *et al.* 2000, Johnson *et al.* 2003). In other cases, the appropriate response to a predator has to be learned. For example, New Zealand Robins *Petroica australis* lived without mammalian predators until the 18th century, and probably do not have a genetic template for the discrimination of mammalian predators. However, Robins on mainland New Zealand respond strongly to introduced stoats, and it has proven easy to train naive, non-responding birds from islands to discriminate and respond to stoats (Maloney & McLean 1995). Innate vs. learned predator discrimination are obviously not mutually exclusive categories, and are expected to operate together for much of the time (e.g. Davies *et al.* 2004, Wiebe 2004). Adaptive responses to variation in levels of predation threat can be enhanced by learning (Griffin 2004), but the extent of learned responses to predators is still unclear.

Here we tested (1) to what extent Arabian Babblers *Turdoides squamiceps* can distinguish between species of avian predators of varying levels of threat (interspecific threat-sensitivity), (2) whether Babblers can distinguish between situations differing in actual level of threat during encounters with predators of high threat level (intraspecific threat-sensitivity) and (3) whether the response of Babblers becomes more appropriate if more information concerning the level of threat of each potential predator is available to them, i.e. if their anti-predation behaviour is influenced by learning. Arabian Babblers are thrush-sized birds resident in the open semi-desert habitat of the Arabian Peninsula (Zahavi 1989, 1990). Groups range from two to 22 (often related) individuals. Outside the nestling feeding period, foraging usually takes place in close proximity to other group members. Whenever the group is foraging in open habitat, one sentinel individual is usually found scanning for danger from a high vantage post, such as a tree or bush (Wright *et al.* 2001a, 2001b, 2001c). All group members share in scanning, which involves taking up an appropriately high sentinel perch position and actively watching the surroundings for various disturbances and threats, but primarily for potential predators. Alarm or mobbing calls are given when a potential predator is observed. Any group member within hearing range usually responds, either by taking cover and scanning for the predator or by approaching the caller to observe the source of disturbance. After the threat has passed, feeding restarts and the original sentinel or a replacement individual resumes scanning (Wright *et al.* 2001a, 2001b, 2001c). Obviously, this system of sentinels requires that individuals are reliable, i.e. capable of appropriately warning the group against dangerous predators, but without giving too many false alarms which unnecessarily disturb important activities such as foraging.

Our study site in the Arava rift valley, Israel, is positioned on a very narrow connection between huge African wintering grounds and Eurasian breeding grounds, and the migration of birds through this area is one of the most intense in the world (Safriel 1968, Moreau 1972). This migration also involves hundreds of thousands of birds of prey, adding to the already present resident raptor species. Some of the migrating raptors rely on energy stores to complete their migrations, whereas other species may hunt during stopover or during migration (Gorney & Yom-Tov 1994, Yosef 1996). Thus, the level of predation threat to Babblers differs between species of raptor. The exposure of the Babblers to the very abundant avian predators is therefore highly diverse in species composition and level of threat posed by each species, as well as variable in time, making the job of a sentinel (to spot all dangerous predators yet avoid false alarms) very demanding, perhaps more so than anywhere else in the world.

METHODS

Data collection

We studied Arabian Babblers at Hatzeva, a 25-km^2 area of desert, located 30 km south of the Dead Sea in the Arava rift valley. From 18 March until 25 May 1996, ten groups of Arabian Babblers (mean group size = 5.3 birds, range = 3–8 birds) were visited regularly for 1–6 h per day (mean number of days spent per group was 3.2). Babbler groups were previously habituated to human observers by Prof. Amotz Zahavi and students from Tel Aviv University (Zahavi 1989, 1990). Habituation to humans allowed distances between observers and sentinels to be typically between 5 and 20 m, with no detectable effects on the behaviour of the birds (see Wright 1997, Wright *et al.* 2001a, 2001c). Sentinels and other group members were always within visual and hearing range. The observer (and the sentinel) continuously scanned the immediate area, and the open nature of the habitat made it possible to record nearly all potentially threatening avian predators. For every sighting of a potential predator, the species, date and relevant details such as flight characteristics and distance to the group were recorded. The response of the sentinel was also recorded as either producing an alarm call or not. Alarm calls for disturbances other than potential avian predators occurred (mammalian predators, a startled hare, a children's balloon drifting past, human activity on nearby agricultural land), but are not included in the analyses here.

In some cases, alarm calls were given for various non-raptors also, which we considered to be non-threatening (such as other passerines). Because these species were often very common, their presence in the local area was not noted continuously, and so only the instances when an alarm call was given were included in the data set. However, field notes and personal experience permitted estimation of the relative abundance of these species during the observation period.

The number of recorded events collected for each individual and/or group of Babblers varied, but was sometimes very low. It was also not always possible to record the exact identity of individual Babblers involved in each alarm-calling event. Therefore, our data cannot be reduced down to measurements per bird prior to analyses, and we are forced to treat each potential predation event as independent. This has the drawback of restricting any interpretation of our statistical analysis with respect to individual adaptation. We also did not estimate the abundance of all potential predators at the group level, but only at the population level, and therefore could not base our analyses on group means. We assume that individuals and groups did not differ in their exposure to predators in time, number or diversity, or in their responses to potential threats. We feel that these assumptions are justified in view of the homogeneous habitat use made by raptors on migration through the study site, the large home ranges of resident birds of prey compared with those of Babblers, and the uniformity of many other behaviours both between and within Babbler groups at this site (e.g. Wright 1997, Wright *et al.* 2001a, 2001c). Moreover, note that there is no false inflation of sample size (degrees of freedom) resulting from pseudo-replication as the statistical analyses are based on average values per predator species, not on the individual observations.

The species-specific level of threat of any predator observed was estimated by looking at literature on diet composition (Brown & Amadon 1968, Glutz von Blotzheim *et al.* 1971, Cramp & Simmons 1980, Forsman 1999). Depending on the proportion of the predator's diet consisting of birds of similar size and type as the Babblers, we scored threat level as low, intermediate or high. Any raptor species of high threat level that does not hunt on migration but instead relies on stored energy deposits (Gorney & Yom-Tov 1994, Yosef 1996) was given a lower, intermediate level of threat. For predators of high threat level, we classified the actual threat of each individual observation on the basis of our general experience of migratory and hunting behaviour in the area: high soaring or gliding (often in groups) is harmless, whereas individuals hovering or flying low and searching the area are threatening. We could also have assessed the level of threat posed by different raptor species on the basis of actual attacks observed, but these were rare and would constitute only a few observations. Aborted attacks were more frequent, and it is possible that actual threat was reduced by the presence of human observers. Such confounding effects of observers are difficult to control for and represent a serious problem in studies that focus on direct measurement of predation rates. However, evidence from observations of Arabian Babblers at this study site (e.g. at various distances) suggests that our methods of observation did not influence any behaviours in the Babblers themselves (Wright 1997, Wright *et al.* 2001a, 2001c), either in time spent scanning or in their response to different kinds of predators. Hence, the Babblers did not appear to act as if they felt safer from predators with people around nor did they base their response to potential predators on the observer's behaviour, so our data probably represent natural responses to potential avian predators.

Data analyses

Test 1: discrimination between harmless and dangerous species

For each species (raptors and non-raptors alike), the number of cases when a Babbler alarm call was given was divided by the (estimated) number of all encounters during our observation bouts. Using these fractions, we were able to test whether the probability of giving alarm calls depended upon the level of threat posed by each species (interspecific threat-sensitivity). Prior to conducting an ANOVA, the probabilities were transformed:

$$P' = 0.5 * (\text{arcsine}(\sqrt{x}/(n+1)) + \text{arcsine}(\sqrt{(x+1)}/(n+1))),$$

where *x* is the number of positive alarm-calling events, and *n* the total number of encounters. This transformation is preferable when probabilities are near 0 or 1 (Zar 1995). We subsequently applied a Bonferroni-adjusted *post-hoc* test to determine which groups differed from each other.

Test 2: discrimination between harmless and dangerous situations

Encounters with predator species that normally pose a high level of threat may have been harmless on some occasions, depending on the specific situation. We tested whether Babblers are sensitive in their anti-predator behaviour to these varying levels of threat as indicated by predator behaviour and circumstance (intraspecific threat-sensitivity). We divided all encounters with predators of high threat level *a priori* into dangerous vs. harmless, and used a Fisher exact test to determine whether Babblers differed in their probability of giving alarm calls relative to the actual level of threat. Because we found positive evidence for such intraspecific threat-sensitivity, we omitted all non-threatening situations with a high-threat predator ($n = 4$) from all other analyses.

Test 3: improving anti-predation behaviour by learning

If the correct response to a potential predator can be improved by the updated assessment of level of threat through repeated encounters (i.e. the level of threat can be learned), then the response behaviour should approach more appropriate levels over time for more common potential predators. We therefore tested how the proportion of alarm calls given changed with the number of encounters, for each of the three groups of predators differing in level of threat, using a Spearman's rank correlation. Specifically, we predicted that the proportion of alarm calls given should remain high or increase for predators of high threat level, but should remain lower or decrease for predators of intermediate and low threat level.

Statistically conservative testing

Obviously, not all potential avian predators will have been recorded, especially if the sentinel itself did not give alarm calls, and therefore the data are necessarily biased towards observations involving alarm calling by the sentinel. This would mean that any level of error by the sentinel (warning for harmless species and missing dangerous predators) would therefore work against the predicted effects (that harmless species provoke a smaller proportion of alarm calls; that non-threatening encounters with dangerous predators are not warned for; that the probability of alarm calling for predators of intermediate or low threat decreases with abundance), making our tests statistically conservative.

RESULTS

We collected data on 122 occasions when an alarm call was given, and on 115 occasions when a potential predator was observed by us but no alarm call was given. In total, 36 bird species were involved in these events; the responses of the Babblers to each species are summarized in Table 1. In all cases when alarm calls were given, group members responded by taking cover and/or scanning and sometimes by joining the sentinel.

Test 1: discrimination between harmless and dangerous species

The probability of alarm calling increased with the level of threat of each species (one-way ANOVA: $F_{2,33} = 13.4$, $P < 0.001$, $r^2 = 0.45$; Fig. 1). The predator

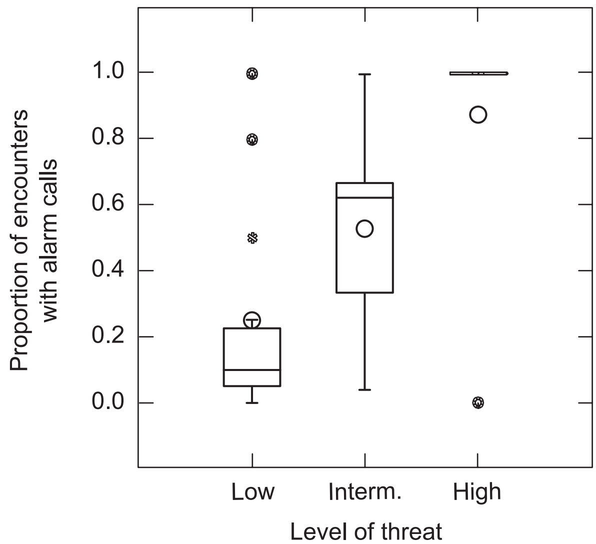

Figure 1. Threat-sensitivity in Arabian Babblers in response to potential predators of low, intermediate or high level of threat (see Table 1 for classification). Response by Babblers is expressed as the proportion of the total number of encounters that provoked alarm calls, for all raptor species observed by us plus non-raptor species that at least once elicited alarm calls from the Babblers. Box-plots illustrate the group average (open circle), the median (horizontal line), the central 50% of the data (25–75 percentile, box), the range of non-outlying observed values (contained within 1.5 times the length of the box starting at the upper or lower limit of the box, vertical line), outliers at more than 1.5 times the length of the box (asterisk) or extreme outliers at more than three times the length of the box (filled circle).

Table 1. Observations and categorizations for all predatory avian species seen close to Arabian Babbler groups, as well as for all bird species for which at least one alarm call was given (i.e. erroneous warnings for non-predators). Predation threat to Babblers was categorized as low, intermediate or high.

Species	No. of warned encounters	No. of total encounters	Proportion of encounters with alarm calls	Threat level	Migratory status
Barbary Falcon *Falco pelegrinoides babylonicus*	4	5	0.80	high	resident
Black Kite *Milvus migrans*	7	11	0.64	intermediate	migrant
Black Stork *Ciconia nigra*	2	2	1.00	low	migrant
Booted Eagle *Hieraaetus pennatus*	0	1	0.00	high	migrant
Brown-necked Raven *Corvus ruficollis*	2	50*	0.04	intermediate	resident
Common Kestrel *Falco tinnunculus*	16	16	1.00	high	resident
Common Swift *Apus apus*	1	20*	0.05	low	migrant
Common Raven *Corvus corax*	4	4	1.00	intermediate	resident
Collared Pratincole *Glareola pratincola*	1	2	0.50	low	migrant
Cretzschmar's Bunting *Emberiza caesia*	1	4	0.25	low	migrant
Eurasian Collared Dove *Streptopelia decaocto*	7	500*	0.01	low	resident
Eurasian Marsh Harrier *Circus aeruginosus*	24	26	0.92	high	migrant
Eurasian Sparrowhawk *Accipiter nisus*	8	8	1.00	high	migrant
European Bee-eater *Merops apiaster*	2	12	0.17	low	migrant
European Honey-buzzard *Pernis apivorus*	4	5	0.80	low	migrant
European Turtle Dove *Streptopelia turtur*	1	20*	0.05	low	migrant
Grey Heron *Ardea cinerea*	0	1	0.00	low	migrant
Isabelline Wheatear *Oenanthe isabellina*	1	10*	0.10	low	migrant
Lesser Kestrel *Falco naumanni*	1	1	1.00	intermediate	migrant
Lesser Whitethroat *Sylvia curruca*	1	50*	0.02	low	migrant
Levant Sparrowhawk *Accipiter brevipes*	5	6	0.83	high	migrant
Long-legged Buzzard *Buteo rufinus*	5	8	0.63	intermediate	migrant
Masked Shrike *Lanius nubicus*	1	10*	0.10	low	migrant
Montagu's Harrier *Circus pygargus*	4	4	1.00	high	migrant
Northern Wheatear *Oenanthe oenanthe*	1	10*	0.10	low	migrant
Pallid Harrier *Circus macrourus*	3	4	0.75	high	migrant
Red-rumped Swallow *Hirundo daurica*	1	10*	0.10	low	migrant
Rufous-tailed Scrub Robin *Cercotrichas galactotes*	1	6	0.17	low	migrant
Scrub Warbler *Scotocerca inquieta*	1	30*	0.03	low	resident
Short-toed Eagle *Circaetus gallicus*	1	3	0.33	intermediate	resident
Southern Grey Shrike *Lanius meridionalis*	4	50*	0.08	intermediate	resident
Steppe Buzzard *Buteo buteo vulpinus*	3	8	0.38	intermediate	migrant
Steppe Eagle *Aquila nipalensis*	2	3	0.67	intermediate	migrant
Woodchat Shrike *Lanius senator*	1	5	0.20	low	migrant
Yellow-legged Gull *Larus michahellis*	1	1	1.00	low	migrant

*The estimated number of total encounters for some non-raptor species.

groups of low and high threat differed significantly (*post-hoc* Bonferroni test: $P < 0.001$), as did the intermediate- and high-threat groups (*post-hoc* Bonferroni test: $P = 0.026$); the difference between the low- and intermediate-threat groups was not significant (*post-hoc* Bonferroni test: $P = 0.150$).

Test 2: discrimination between harmless and dangerous situations

Four encounters with a predator of high threat level were classified by us as harmless: a Barbary Falcon *Falco peregrinoides* flying past with prey in its talons and thus unlikely to attack again; a clearly migrating Pallid Harrier *Circus macrourus*, and a Eurasian Sparrowhawk *Accipiter nisus*, as indicated by circling and gliding high in the sky; and a group of Levant Sparrowhawks *Accipiter brevipes* thermaling in a large group high in the sky. In three of these four encounters, no alarm call was given even though the sentinel had spotted the potential predator, whereas for 20 high-threat encounters with these same four species alarm calls were always given (Fisher exact test: $P = 0.002$).

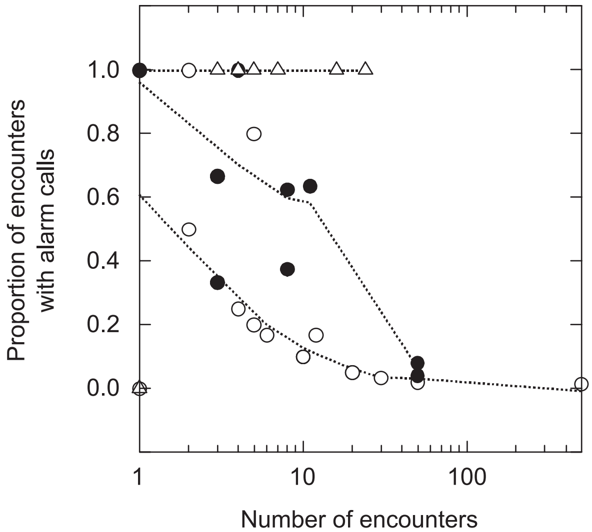

Figure 2. Probability that Babblers gave alarm calls as a function of predator abundance, for potential predator species differing in level of threat: low (open circles), intermediate (filled circles) or high (triangles). On the *y*-axis is the proportion of all encounters when Babblers gave alarm calls; the *x*-axis gives the number of encounters (on a log-scale for graphical purposes). Because several points overlap, a line representing the running mean was fitted to illustrate the trends (using the LOWESS procedure in SYSTAT, tension 0.9).

Test 3: improving anti-predation behaviour by learning

Figure 2 shows the relationship between the number of encounters with a potential predator and the probability of alarm calling. For species of high threat, the Babblers always responded by alarm calling (except for a single encounter with a Booted Eagle *Hieraaetus pennatus*). The probability of giving alarm calls thus remained rather constant per species despite variation in the number of encounters per species (Spearman's rank correlation: $r = 0.38$, $n = 8$, $P = 0.390$). For species of intermediate threat, the probability of responding declined significantly with number of encounters (Spearman's rank correlation: $r = -0.79$, $n = 9$, $P = 0.012$). For species of low threat, the probability of responding declined non-significantly with number of encounters (Spearman's rank correlation: $r = -0.22$, $n = 19$, $P = 0.360$).

DISCUSSION

Test 1: discrimination between harmless and dangerous species

Arabian Babblers seem to be able to discriminate between species differing in level of potential predation threat. This effect was actually more pronounced than it appears in the data presented here, because the Babblers never gave alarm calls to dozens of harmless species occurring in the area, which therefore went unrecorded in our data set. However, despite the obvious lack of danger, alarm calls were sometimes given in response to non-threatening species. This remained at a relatively low frequency (Fig. 1) and occurred mainly for species with which the Babblers had only low frequencies of encounters (Fig. 2). We would therefore have to conclude that these were errors in predation threat assessment by the Babblers (see below). By contrast, all species of raptors provoked alarm calls on at least one occasion (with the exception of the single Booted Eagle sighting).

Test 2: discrimination between harmless and dangerous situations

Within the subset of encounters with raptors of high threat where we could distinguish between encounters of low and high threat, the Babblers did indeed respond to apparent intraspecific variation in threat. This shows that Babblers not only discriminated between the different levels of threat posed by different species of raptors and other birds (interspecific threat-sensitivity), but that they were also capable of the more demanding task of distinguishing between levels of threat during encounters with each of those species (intraspecific threat-sensitivity).

Test 3: improving anti-predation behaviour by learning

Support for learning in shaping the response of Arabian Babblers to predators differing in level of threat was provided by the data in Figure 2. It should, however, be noted that part of the observed (and non-significant) decline in the group of low threat may have been an artefact. Many uncommon low-threat species were not included in the data set as they were never warned for, thus biasing the line upward for uncommon species. By contrast, we feel that for species of intermediate threat the significant decline does represent learning, as all species of intermediate threat were included in the data set, whether Babblers were ever recorded to give alarm calls or not. Hence, the Babblers seemed to have learnt progressively that some of the more common predators had a lower level of threat than initially assessed, and that it was appropriate to reduce their anti-predator response accordingly. Simple, non-adaptive habituation to predators could be seen as an alternative explanation for this decline in response to common predators of intermediate threat level. However, this is not supported by the same high level of response recorded for common predators of high threat level. Therefore, adaptive assessment and learning regarding the level of threat posed by different predators seems to have been involved in the fine-tuning of Babbler alarm-calling propensity. It further seems likely that at least part of this learning is a form of social learning, i.e. learning by observing the behaviour of others (Griffin 2004), especially in a species such as the Arabian Babbler with permanent social groups and a system of rotating sentinels. Social learning about predators has received relatively little attention from biologists (but see Griffin 2004), but it is conceivable that it may contribute to the benefits of living in groups and may thus contribute to the evolution of co-operative breeding, especially in habitats with an ever-shifting abundance and diversity of predators.

Over- and underestimation of predation threat

It is clear that a certain percentage of 'mistakes' were made by Arabian Babblers when alarm calling. In most such cases, a harmless species of bird was either flying straight towards the sentinel or suddenly appeared out of cover very close to the sentinel (triggering either a species-misidentification based on suspicious behaviour, or a misidentification of the intentions of a correctly identified bird). Therefore, we interpret these as threat assessment mistakes, possibly reflecting the Babblers' adaptive tendency to warn cautiously for any and all events that might pose a threat until it can be decided otherwise. Babblers often gave alarm calls in response to unusual but harmless species or events (e.g. the rather alien sight of a red children's balloon drifting past, a stooping European Bee-eater *Merops apiaster*, or an immature Yellow-legged Gull *Larus michahellis*: the latter two possibly resembling a raptor). However, they virtually never failed to give an alarm call in the case of a potentially threatening situation (the single Booted Eagle event remains the only exception here). Overall, the Babblers often overestimated but rarely underestimated predation threat. This observation supports predictions made by Bouskila and Blumstein (1992) based upon a dynamic optimization model of vigilance, which assumes that individuals do not have perfect information on levels of threat regarding every encounter. In such a situation, individuals do best by overestimating the level of threat, as a false alarm is much less costly than wrongly classifying an attacking predator as harmless.

Why did Babblers not always respond to predators of intermediate or high threat? We have already shown that dangerous predators behaving harmlessly were ignored, and this was probably in order to avoid disturbing the foraging or other behaviours of group members unaware of the presence of these predators ('economic' hypothesis: the reaction depends on a balancing of costs and benefits, Quinn & Cresswell 2005). On the other hand, it is also possible that dangerous predators behaving harmlessly and predators of intermediate threat could not always be correctly identified as potential predators ('perceptual limit' hypothesis: the reaction limitations depend on the detection limitations, Quinn & Cresswell 2005). With the data at hand we cannot easily distinguish between these hypotheses, but we think that economic decisions seem to be playing the more important role. In virtually all cases Babblers did give alarm calls to 'harmless' circling or gliding raptors of high threat that were resident (and hence might be hunting in the area in the near future) but did not give alarm calls to similarly behaving migrant raptors of high threat (sparrowhawks, harriers), indicating that the same flight pattern (same detection limits) triggered different responses for resident vs. migrant raptor species (different costs and benefits).

This study shows adaptive sensitivity to variation in predation threat in the anti-predation behaviours of Arabian Babblers, both between and within species of potential predators. Moreover, Babbler groups adjusted their responses dynamically and approached more appropriate levels of alarm calling when provided with more information on each species over time due to repeated encounters. This is no small achievement, as the Arabian Babblers' environment presents them with possibly the world's greatest variation in number and species of potentially threatening avian predators. These observations agree with the basic predictions of theory concerning anti-predation behaviour according to level of threat: high-threat species more often provoked alarm calls than species of lower threat; situations of low threat were ignored even when they involved normally highly threatening species; and there was evidence of over-response to potential threats posed by novel stimuli and/or situations that contained insufficient information, with subsequent adjustment as more information became available.

We would like to thank Amotz Zahavi for the opportunity to work on his wonderful birds, and for the ringing and population monitoring efforts of his group at Hazeva. We thank Rob Bijlsma and Kees Camphuysen for providing some of the literature used, and Dan Blumstein for discussion. We thank Will Cresswell, Jeremy Green and an anonymous reviewer for their comments on a previous version. J.W. was funded by a NERC postdoctoral fellowship.

REFERENCES

Albrecht, T. & Klvana, P. 2004. Nest crypsis, reproductive value of a clutch and escape decisions in incubating female mallards *Anas platyrhynchos*. *Ethology* **110**: 603–613.

Blumstein, D.T., Fernandez-Juricic, E., LeDee, O., Larsen, E., Rodriguez-Prieto, I. & Zugmeyer, C. 2004. Avian risk assessment: effects of perching height and detectability. *Ethology* **110**: 273–285.

Bouskila, A. & Blumstein, D.T. 1992. Rules of thumb for hazard assessment: predictions from a dynamic model. *Am. Nat.* **139**: 161–176.

Brown, L. & Amadon, D. 1968. *Eagles, Hawks and Falcons of the World*. Cambridge: Hamlyn Publishing Group.

Cavanagh, P.M. & Griffin, C.R. 1993. Responses of nesting Common Terns and Laughing Gulls to flyovers by large gulls. *Wilson Bull.* **105**: 333–338.

Cramp, S. & Simmons, K.E.L. (eds) 1980. *The Birds of the Western Palearctic*, Vol. 2. Oxford: Oxford University Press.

Cresswell, W. 1993. Escape responses by redshanks, *Tringa totanus*, on attack by avian predators. *Anim. Behav.* **46**: 609–611.

Davies, N.B., Madden, J.R. & Butchart, S.H.M. 2004. Learning fine-tunes a specific response of nestlings to the parental alarm calls of their own species. *Proc. R. Soc. Lond. B* **271**: 2297–2304.

Forsman, D. 1999. *The Raptors of Europe and the Middle East*. London: T. & A.D. Poyser.

Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. 1971. *Handbuch der Vögel Mitteleuropas.* Band 4. Wiesbaden: Akademische Verlagsgesellschaft.

Gorney, E. & Yom-Tov, Y. 1994. Fat, hydration condition, and moult of Steppe Buzzards *Buteo buteo vulpinus* on spring migration. *Ibis* **136**: 185–192.

Griffin, A.S. 2004. Social learning about predators: a review and prospectus. *Learning Behav.* **32**: 131–140.

Helfman, G.S. 1989. Threat-sensitive predator avoidance in damselfish–trumpetfish interactions. *Behav. Ecol. Sociobiol.* **24**: 47–58.

Johnson, F.R., McNaughton, E.J., Shelley, C.D. & Blumstein, D.T. 2003. Mechanisms of heterospecific recognition in avian mobbing calls. *Austr. J. Zool.* **51**: 577–585.

Kleindorfer, S., Fessl, B. & Hoi, H. 2005. Avian nest defence behaviour: assessment in relation to predator distance and type, and nest height. *Anim. Behav.* **69**: 307–313.

Lima, S.L. & Bednekoff, P.A. 1999. Temporal variation in danger drives antipredator behaviour: the predation risk allocation hypothesis. *Am. Nat.* **153**: 649–659.

Maloney, R.F. & McLean, I.G. 1995. Historical and learned predator recognition in free-living New Zealand robins. *Anim. Behav.* **50**: 1193–1201.

Moreau, R. 1972. *The Palearctic-African Bird Migration Systems*. London: Academic Press.

Quinn, J.L. & Cresswell, W. 2005. Escape response delays in wintering redshank, *Tringa totanus*, flocks: perceptual limits and economic decisions. *Anim. Behav.* **69**: 1285–1292.

Safriel, U. 1968. Bird migration at Eilat, Israel. *Ibis* **110**: 283–320.

Sordahl, T.A. 2004. Field evidence of predator discrimination abilities in American Avocets and Black-necked Stilts. *J. Field Ornith.* **75**: 376–385.

Vasquez, R.A. & Kacelnik, A. 1998. Animal foraging: more then met the eye. *Trends Ecol. Evol.* **13**: 110–111.

Veen, T., Richardson, D.S., Blaakmeer, K. & Komdeur, J. 2000. Experimental evidence for innate predator recognition in the Seychelles warbler. *Proc. R. Soc. Lond. B* **267**: 2253–2258.

Wiebe, K.L. 2004. Innate and learned components of defence by flickers against a novel nest competitor, the European starling. *Ethology* **110**: 779–791.

Wright, J. 1997. Helping-at-the-nest in Arabian Babblers: signalling social status or sensible investment in chicks? *Anim. Behav.* **54**: 1439–1448.

Wright, J., Berg, E., de Kort, S.R., Khazin, V. & Maklakov, A.A. 2001a. Safe selfish sentinels in a cooperative bird. *J. Anim. Ecol.* **70**: 1070–1079.

Wright, J., Berg, E., De Kort, S.R., Khazin, V. & Maklakov, A.A. 2001b. Cooperative sentinel behaviour in the Arabian Babbler. *Anim. Behav.* **62**: 973–979.

Wright, J., Maklakov, A.A. & Khazin, V. 2001c. State-dependent sentinels: an experimental study in the Arabian Babbler. *Proc. R. Soc. Lond. B* **268**: 821–826.

Yosef, R. 1996. Raptors feeding on migration at Eilat, Israel: opportunistic behaviour or migratory strategy? *J. Raptor Res.* **30**: 242–245.

Zahavi, A. 1989. Arabian Babbler. In Newton, I. (ed.) *Lifetime Reproduction in Birds*: 254–275. London: Academic Press.

Zahavi, A. 1990. Arabian Babblers: the quest for social status in a cooperative breeder. In Stacey, P.B. & Koenig, W.D. (eds) *Cooperative Breeding in Birds: Long Term Studies of Ecology and Behaviour*: 103–130. Cambridge: Cambridge Univiversity Press.

Zar, J.H. 1995. *Biostatistical Analyses*. New York: Prentice Hall International Editions.

Received 16 June 2005; revision accepted 31 January 2006.