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ORIGINAL ARTICLE

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Do responses of galliform birds vary adaptively with predator size?

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Abstract Past studies of galliform anti-predator behavior show that they discriminate between aerial and ground predators, producing distinctive, functionally referential vocalizations to each class. Within the category of aerial predators, however, studies using overhead models, video images and observations of natural encounters with birds of prey report little evidence that galliforms discriminate between different raptor species. This pattern suggests that the aerial alarm response may be triggered by general features of objects moving in the air. To test whether these birds are also sensitive to more detailed differences between raptor species, adult chickens with young were presented with variously sized trained raptors (small, intermediate, large) under controlled conditions. In response to the small hawk, there was a decline in anti-predator aggression and in aerial alarm calling as the young grew older and less vulnerable to attack by a hawk of this size. During the same developmental period, responses to the largest hawk, which posed the smallest threat to the young at all stages, did not change; there were intermediate changes at this time in response to the middle-sized hawk. Thus the anti-predator behavior of the adult birds varied in an adaptive fashion, changing as a function of both chick age and risk. We discuss these results in light of current issues concerning the cognitive mechanisms underlying alarm calling behavior in animals.

Keywords Alarm calls · Anti-predator behavior · Galliforms · Size discrimination

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Introduction

In response to the intense selection pressures imposed by predation, prey animals have evolved many adaptations for reducing its impact (Curio 1976; Edmunds 1974; Endler 1986, 1991). When detected by a predator, a potential prey animal has several options for minimizing the chances of capture. It can avoid detection by cryptic behavior and use cover to the same end. If detected, it may flee immediately or wait until attack is imminent and then strive to avoid capture by last minute evasion (Palleroni, unpublished data). Depending on the circumstance, it may signal to the predator that it has been detected with behavior designed to alert the predator to the prey's vigilance. Yet another option, sometimes overlooked, is to threaten or advance on the predator. The potential prey may even attack or repel the predator, a viable strategy if the animal preyed upon has effective ways of defending itself. A small predator will be more vulnerable to counterattack by prey than a large one. A critical consideration is the relative size of the predator, but few studies have explored whether prey ever discriminate among predators of a particular type based on their size (Evans et al. 1993). In fact, some studies of galliforms (Gyger et al. 1987; Palleroni, Evans and Marler, unpublished data) have suggested that individuals pay little attention to the size of an aerial predator, even though they give distinctive calls to aerial predators (e.g., a soaring hawk) as opposed to ground predators (e.g., a ferret).

Among species of birds and mammals that produce distinctive vocalizations in response to particular classes of predators, such as aerial and terrestrial predators (Seyfarth et al. 1980a, b; Sherman 1985; Seyfarth and Cheney 1990; Macedonia and Polak 1989; Marler et al. 1992; Macedonia and Evans 1993), some are also known to discriminate between different birds of prey. Seyfarth and Cheney (1980b) found that vervet monkeys (*Chlorocebus aethiops*) distinguish between different species of aerial predators flying overhead, giving more "eagle" alarm calls to those raptor species which hunt vervets, as well as to other raptors which resemble them in appearance. During development, infant vervets give eagle alarm calls to a broader range of species than do adults, including even leaves, but with experience, the eliciting class of stimuli is refined. Evans et al. (1993) used video images with chickens to demonstrate that the size of the stimulus significantly potentiated aerial alarm calling. However, none of these studies focused specifically on the effects of varying raptor size, or the significance of the relationship between the size of actual raptors and vulnerability of the prey species under study. One reason for the lack of systematic research on this issue is that prior studies have used either natural observations of predator events or highly controlled and often artificial stimuli in the laboratory. We address both the theoretical and methodological issues in the following paper by using trained raptors of different sizes.

We chose as potential prey golden Sebright bantams because, like the red jungle fowl, they are sexually size dimorphic with males, females and young corresponding to the optimal sizes preyed upon by each of the three predators used in this experiment (small: sharp-shinned hawk, *Accipiter striatus*; medium: Cooper's hawk *Accipiter cooperii*; large: goshawk (*Accipiter gentilis*). The range of optimal prey size corresponding to these three accipiters has little overlap. A female goshawk's optimal prey size is closer to the male golden Sebright and although smaller prey can be taken by female goshawks, the likely target is the more conspicuous male since size is not a deterrent here. The female Cooper's hawk is more likely to be deterred by male bantams since their size is outside the range of prey taken and the rooster's spurred attacks are effective with a predator smaller than itself. A female bantam lies within the optimal prey size of a female Cooper's hawk. The male sharp-shinned hawk typically catches prey the size of the bantam chicks and female chickens are far larger than prey taken by males.

Methods

Subjects were nine pairs of golden Sebright bantam chickens and their broods totaling 73 birds, studied from May to June 1994 at the University of California, Davis. Golden Sebrights are a strain of bantam chickens closely related to the ancestral jungle fowl, with which they have many behavioral traits in common (Collias and Joos 1953; Kruijt 1964; Collias and Collias 1967; Stokes 1971; Sherry 1977). They are less wild and therefore more tractable as experimental subjects. The anti-predator behavior we describe is generally similar to what has been reported in a range of galliform species, including grouse (Goethe 1940; Muller 1961), turkeys (Schleidt 1961a, b) and pheasants (McNiven 1960), as well as in ducks and geese (Lorenz 1939; Tinbergen 1948; Melzack et al. 1959), but we cannot exclude the possibility that domestication has had some influence on their anti-predator behavior.

The University of California, Davis Institute of Ecology field facility where the studies were conducted is located on Putah Creek, Davis, California, an oak-edged riparian corridor surrounded by open fallow agricultural fields. The adults had been raised the previous year with parents in large open-air outdoor enclosures (7 m × 14 m). The area abounded with native aerial predators including migrant sharp-shinned hawks, Cooper's hawks, red-tailed hawks (*Buteo jamaicencis*), Swainson's hawks (*B. swainsoni*), ferruginous hawks (*B. regalis*), red-shouldered hawks (*B. platypterus*), kestrels (*Falco sparverius*), peregrine falcons (*F. peregrinus*), northern harriers (*Circus cyaneus*) and white-tailed kites (*Elanus leucurus*), but one of the "stimulus" species used, the goshawk, was not observed. Other birds such as common crows (*Corvus brachyrhynchos*) and yellow-billed magpies (*Pica nuttali*) were common in the area.

The nine broods ranged from 5 to 12 chicks. To establish the family groups, most chicks were hatched artificially and put under broody hens, placed with them within 1 day of hatching. Most of the adult male foster parents were matched with a hen prior to hatching on the basis of their close association with her while incubating, particularly when feeding. In addition, some adult males were chosen for pairing with hens and their broods according to their attentiveness to a given hen as she escorted her brood. Pairs and their broods were transferred, each to their own 3 m × 4 m outdoor enclosure, 1 day after hatching.

The hawks used as predatory stimuli were on loan from the University of California, Davis Raptor Center, and from a separate study of goshawk breeding biology. For experimental purposes, we tethered the hawks with leather leg bracelets and attached a thin 20-m woven nylon line, anchored with a 200-g weight. We trained two of the hawks to fly in the direction of a lone oak tree with a low (2 m) limb 10 m away and garnished with a meat reward. The sharp-shinned hawk performed consistently with no inducement. The hawks were released from behind a 3 m × 2 m plywood blind and retrieved by hand after the test. The distance from the release point to the oak tree was gradually increased from 1 m to 10 m with an average of 10 trials each before experiments commenced. The test area was between the blind and the oak tree.

All three hawks were in immature plumage, with vertical brown streaks ventrally and uniformally dark brown dorsally. Consequently, they were similar to each other in appearance, except for the size difference (Fig. 1). The sharp-shinned hawk , a male, weighed about 97 g and measured 23 cm from beak to tail. The Cooper's hawk was a female, weighed 480 g and measured 51 cm (i.e., roughly crow-sized). The goshawk, also a female, weighed 970 g and measured 62 cm long. These three accipiters, all bird hunters, were chosen as predatory stimuli because they were similar in shape, coloration and hunting style. Their similarities are such that distinguishing them in the field is challenging when their relative size cannot be determined. Their flight invariably includes four to five wing flaps interspersed with a glide and the attack style of all three is low and direct.

The hawks were released on a tether to fly over and alight near pairs of adult chickens and their young. One additional reason for choosing these particular hawk species is that they varied in size in relation to roosters, hens and chicks in such a way that they ranged from no risk to high risk

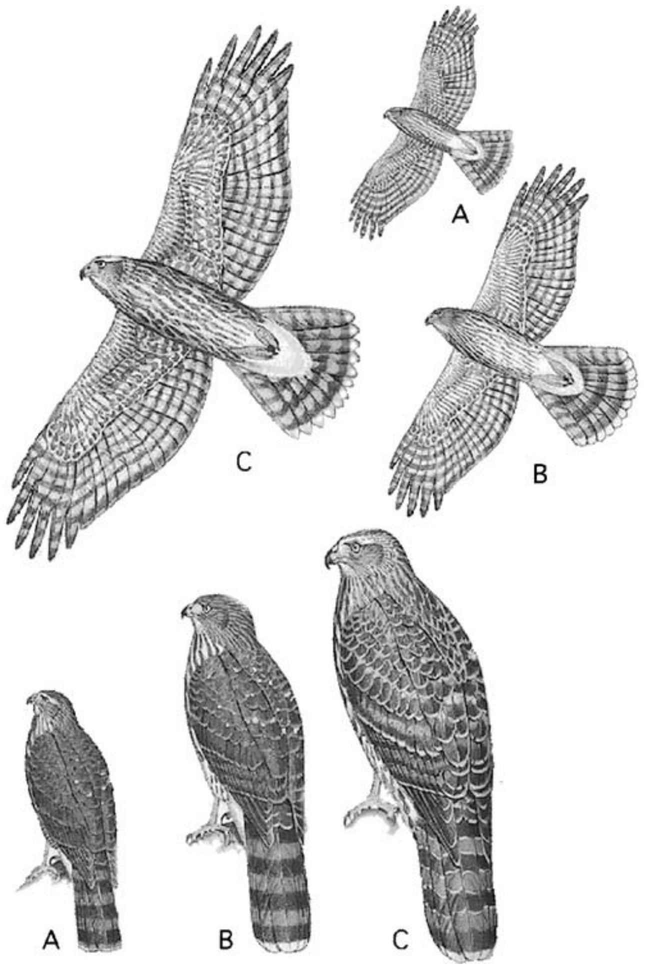

Fig. 1 The three hawks utilized in the experiment: **a** male sharp-shinned hawk (*Accipiter striatus*), **b** female Cooper's hawk (*Accipiter cooperii*) and **c** female goshawk (*Accipiter gentilis*). Drawings modified by (**a**). Palleroni after Clark and Wheeler (1987)

predators. The smallest raptor used, the sharp-shinned hawk, was a male, which is the smaller sex in this sexually size dimorphic family. Cooper's hawks are significantly larger than sharp-shinned hawks and we used the larger female. The largest raptor used in this study was a female goshawk.

On each test day, chickens with their young were moved from their home cage in a portable animal kennel and released on bare ground 5 m from the oak tree and 1 m from a patch of grass 10–20 cm high. Food and water were provided to encourage parents to assemble about 1 m from grass cover. Scattered mealworms were used to induce the birds to gather in the test area. Tests were conducted between 0630 and 0800 hours. Hawks were released 30–45 min after subjects aggregated near the food and water. If subjects wandered away or displayed alarm behaviors during the 15-min interval prior to a presentation, the test was aborted, birds returned to the home cage and testing resumed the next day. Each hawk approach flight lasted about 5 s. Responses were videotaped by an assistant for 10 min prior to release as a control and 10 min after releasing the predator. The video camera was placed 8 m from the focal area and the perched predator so that both were in the field of view. An assistant recorded sounds on the video sound track and also with a Nagra III tape recorder and Sennheiser MK816T with a windscreen-covered microphone pointed at the focal area 4 m away. Videotapes were reviewed on a Panasonic AG-7500 video player with a Panasonic AG-A750 edit recorder and a Panasonic CT-1331Y color monitor. The Nagra sound recordings were consulted only when a call type was difficult to identify by ear.

Each family group, consisting of a pair of chickens and its brood, was tested once every other day, each time with a different species of hawk (sharp-shinned hawk, Cooper's hawk and goshawk) for a total of 15 trials. Chickens were tested in five blocks, one block per week, with the three hawks selected randomly such that all three were used each week. Testing commenced when chicks were 2 days of age and ended at 5 weeks of age spanning the transition from a "broody" to a "non-broody" state that females undergo as their chicks mature. After each test chickens were returned to their outdoor aviaries. Between test days they were fed and watered in the same manner as on test days, including the offering of preferred food items each morning.

Data coding and analyses

Video and audio recordings of the responses of the chickens responding to the three hawks as they flew towards them and landed were analyzed for non-vocal and vocal responses. Scoring was done blind by one assistant trained to identify the behaviors and who had not otherwise participated in the experiment. Reliability was checked against the experimenter's scores for all of the data with no discrepancies. Data from each test were analyzed in two periods, for the first 4 s after hawk presentation, when the hawk was in flight (the flight phase), and for the following 56 s, when the hawk was perched in view of subjects (the perched phase). Calls and other behaviors that began in the flying phase of the trial were allotted to that phase. Vocal response categories of adults included aerial alarm calls, ground alarm calls and other calls.

Non-vocal responses included the subjects' posture, whether or not they gazed steadily at the predator or elsewhere and how long they engaged in these behaviors. Postures were divided into: (1) crouching with sleeking, (2) standing erect with neck extended, (3) ruffled feathers and fanned tail, (4) attack, or (5) no change.

1. During crouching and sleeking, more likely to occur after the birds had run to cover than when they were out in the open, the birds froze and behaved cryptically, with feathers held tight to the body, head often lower than the back, with body motionless, and little to no head movement. Subjects often bent their legs under them as they crouched, allowing for sudden, rapid take-off when approached closely.
2. Erect postures were associated with conspicuous behavior, often accompanied by quick movements interspersed with brief pauses, head pumping and a strutting,

high stepping walk, setting the stage for striking with the spurs.

3. Birds in the ruffled posture moved around actively, and appeared to be in an aggressive state and ready to attack. Attacks were always preceded by this posture. The body was held low, neck feathers were raised, and birds often walked in a figure-eight pattern facing the predator, turning their back towards it only briefly. A hen in the ruffled posture circled through her chicks, sometimes kicking them aside as she darted through them.
4. During attacks the bird would run or fly towards the hawk with feathers raised, sometimes making contact with and knocking the hawk from its perch. About half of the attacks were incomplete, the parent returning to the vicinity of the chicks. Often several rushes were made at the hawk in a short interval of time, seemingly triggered by movements of the predator on its perch. In two instances, the sharp-shinned hawk was knocked from its perch and both adult chickens joined in a rush towards it on the ground. These trials were immediately aborted to protect the hawk.

Gazing directly at the predator through 90° laterally was scored as "looking towards." Looking less than 90° to the rear was scored as "looking away." When gazing at the predator subjects always aimed one eye at the predator, often switching from one eye to the other. During looking away there was little head movement. When birds crouched and sleeked they usually, though not always, gazed away from the predator. Birds in the erect or ruffled feather postures usually gazed towards the predator, an escalation from an erect posture. However, not all postures could be arranged in a linear progression from a mild to a strong response because sleeking and crouching could be considered at either end of the spectrum.

We used BMDPPR (BMDP/Dynamic release 7.0, SPSS, Chicago, Ill.) to run step-wise polychotomous logistic regressions. This model was used because it makes no assumptions about how the parameters are related, the dependent variable is treated as nominal, and there is no actual replication or repeated measures as it extracts only one categorical response from the combination of treatment factors as each blocked pair, trial, and stimulus has only one categorical response. In this sense, it is like the more classical Friedman test, but allows for multiple treatment conditions. Data on adult pairs of chickens were grouped together so that each pair was treated as a unit. Furthermore, in addition to having measurements for pairs varying with respect to only a single treatment, they were also arranged so that they differed with respect to the type of stimulus (hawk), sex of the subject and the temporal positioning of the trial in the series. Pairs were therefore treated as a main effect with the species of hawk, sex of the subject and temporal positioning in the series as second order interactions. All statistical tests are two-tailed with α set at 0.05. In discussing the results, we refer to the three predators as the "small," "medium" and "large" hawks, corresponding to the sharp-shinned hawk, the Cooper's hawk and goshawk, respectively.

Results

Non-vocal responses to the three hawks (see Fig. 2b, c)

First, we consider the responses of both sexes tested as pairs with hawks both in flight and perched, summed for all trials. The results revealed several significant differences (Table 1). Sleeking and crouching behavior were more likely to be given to the larger hawk and an erect posture with ruffling was more likely to be given to the smaller hawk. Intermediate postures were given to the medium sized hawk. Gaze direction also differed significantly in that pairs looked towards the smaller predator and away from the larger predator. Thus, it is clear that the three hawks elicited different responses. Next, we consider male and female responses separately and how they responded to hawks that were perched and hawks in flight.

Looking separately at female non-vocal responses to hawks in flight, the data for the first 4 s of each trial show that females responded significantly differently to the three hawks (Table 2) with significant pair-wise differences. When the small hawk was compared to the medium hawk, non-vocal responses were significantly different. When the small hawk was compared to the large hawk, significant differences were also found. However, there were no significant differences in female responses between the medium hawk and the large hawk. Response differences included more sleeking, crouching and gazing away from the larger predators, and ruffled or erect postures and gazing towards the smaller one (Table 2).

Male non-vocal responses also showed significant differences to hawks for all pair-wise comparisons of hawk species. Unlike females, however, differences were found in the responses to the medium and large hawks. As in females, they responded with more sleeking and crouching and gazing away with the larger predators and ruffled or erect postures and gazing towards the smaller one (Table 2).

Non-vocal responses to the perched hawks were documented separately. Female postures towards the three hawks when perched (4 s–1 min of each trial (Table 2) also differed. Gaze direction differed significantly in response to the three perched hawks with females gazing most at the small hawk, less to the medium sized hawk and least to the large hawk (Table 2). When hawks were compared pair-wise, both postures and gaze direction varied. Significant differences were found between the small

Table 1 Comparison of responses to the three hawks, male sharp-shinned hawk (*Accipiter striatus*), female Cooper's hawk (*Accipiter cooperii*) and female goshawk (*Accipiter gentilis*). Values from polychotomous logistic regression (all hawks, all trials, and all subjects, n=9)

Response	Chi-square	*df*	*P* value
Postures	46.75	16	0.0001
Gaze direction	51.08	16	0.0001
Vocal alarms	54.25	24	0.0001

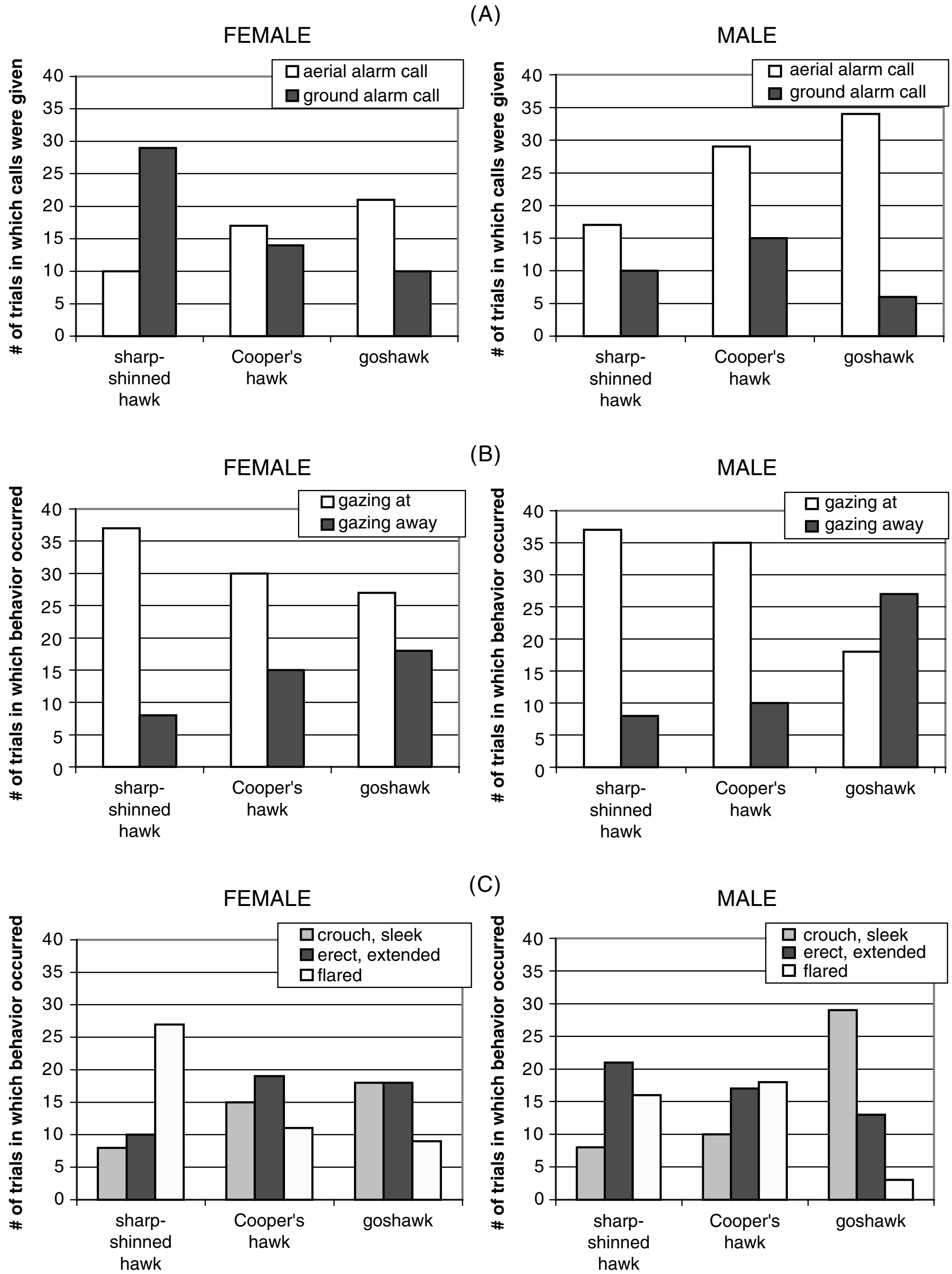

Fig. 2 Total responses for each trial (flying and perched). For each graph n=9 adult chickens, trials =15 (5 per hawk), total =135 (45 per hawk): **a** vocal response: alarm calls, **b** non-vocal response: gaze, **c** non-vocal response: posture

hawk and the medium hawk and the small hawk and the large hawk. As with the hawks in flight, females showed no significant differences between the medium hawk and the large hawk. Gaze direction also differed in response to the small hawk and the large hawk but there were no significant differences between the medium and large hawk. In general, in responding to the perched hawks, females gave more erect postures and more ruffling responses to the smaller hawk and more crouching and sleeking to the larger ones.

As with the females, male non-vocal responses to the perched hawks also differed significantly (Table 2). Like females, males were more likely to stand erect or ruffled in response to the smaller hawk, and to crouch and sleek in response to the larger hawk. Responses to the medium hawk were intermediate. Gaze direction also differed in response to the three perched hawks, with males gazing at the small hawk most, the medium sized hawk less and the large hawk least of all. Non-vocal responses differed significantly in all pair-wise comparisons. Unlike females, males responded differently to the medium and large hawks.

Table 2 Chi-square values for polychotomous logistic regression testing for differences in the above groups: *ALL hawks* between all hawks, *SSH* sharp-shinned hawk, *CH* Cooper's hawk, *GH* goshawk

Type	Response	Sex	ALL hawks	SSH vs. CH	SSH vs. GH	CH vs.GH
In flight (0–4 s)						
Non-vocal	Postures	Female	25.50	10.45	24.38	4.23
			$P<0.001$	$P<0.01$	$P<0.01$	$P<0.12$
			$df=2$	$df=2$	$df=2$	$df=2$
		Male	23.53	10.79	10.01	14.01
			$P<0.001$	$P<0.01$	$P<0.01$	$P<0.01$
			$df=2$	$df=2$	$df=2$	$df=2$
	Gaze	Female	31.11	11.96	25.11	4.23
			$P<0.001$	$P<0.01$	$P<0.0001$	$P<0.12$
			df =2	df =2	df =2	df =2
		Male	23.9	14.97	9.05	15.10
			$P<0.001$	$P<0.01$	$P<0.01$	$P<0.01$
			$df=2$	$df=2$	$df=2$	$df=2$
Vocal	Alarm calls	Female	51.39	23.84	33.75	6.78
			$P<0.001$	$P<0.0001$	$P<0.0001$	$P<0.141$
			$df=3$	$df=3$	$df=3$	$df=3$
		Male	51.24	16.61	19.11	9.89
			$P<0.0001$	$P<0.001$	$P<0/001$	$P<0.02$
			$df=3$	$df=3$	$df=3$	$df=3$
Perched (4 s–1 min)						
Non-vocal	Postures	Female	27.36	11.58	15.37	3.87
			$P<0.001$	$P<0.01$	$P<0.01$	$P<0.15$
			$df=2$	$df=2$	$df=2$	$df=2$
		Male	22.14	10.45	40.67	15.45
			$P<0.001$	$P<0.01$	$P<0.0001$	$P<0.01$
			$df=2$	$df=2$	$df=2$	$df=2$
	Gaze	Female	30.01	12.75	28.07	5.25
			$p<0.001$	$p<0.01$	$p<0.0001$	$p<0.12$
			$df=2$	$df=2$	$df=2$	$df=2$
		Male	24.10	15.37	10.34	16.93
			$P<0.001$	$P<0.01$	$P<0.01$	$P<0.01$
			$df=2$	$df=2$	$df=2$	$df=2$
Vocal	Alarm calls	Female	41.98	17.77	23.45	9.89
			$P<0.001$	$P<0.001$	$P<0.001$	$P<0.02$
			$df=3$	$df=3$	$df=3$	$df=3$
		Male	32.56	10.34	30.79	9.92
			$P<0.001$	$P<0.01$	$P<0.0001$	$P<0.01$
			$df=3$	$df=3$	$df=3$	$df=3$

Non-vocal responses in the "broody" and "non-broody" phases

Thus far, we have presented the results from pooled data, thereby excluding the possible effects of trial number and chick age. The parental behavior of female chickens is distinctly different when they are "broody," during incubation and for about 3 weeks after hatching of the eggs. In particular, they only give the aerial alarm call while they are broody (Karakashian et al. 1988). This phase is equivalent to trials 1–9. Here we compare non-vocal responses during trials 1–9, the "broody" phase, with trials 10–15, the "non-broody phase." We consider female responses first.

Adult female postures differed significantly from the broody to the non-broody phase. Broody females ruffled or stood erect much more and crouched and sleeked much less than when non-broody (Fig. 3a, b). They also gazed at the smaller hawks much more during the broody phase than during the non-broody phase (Fig. 4a, b). Females attacked the hawks frequently while broody (Fig. 5). Attacks were restricted to the earliest trials when young were 3 weeks post-hatching or younger. For example, there were 15 cases of females attacking the sharp-shinned hawk (the smallest) in the first three trials and none in the latter two trials. At this same time, broody females were much less likely to attack the large hawk with intermediate frequencies of attack in response to the medium hawk. Females, showed

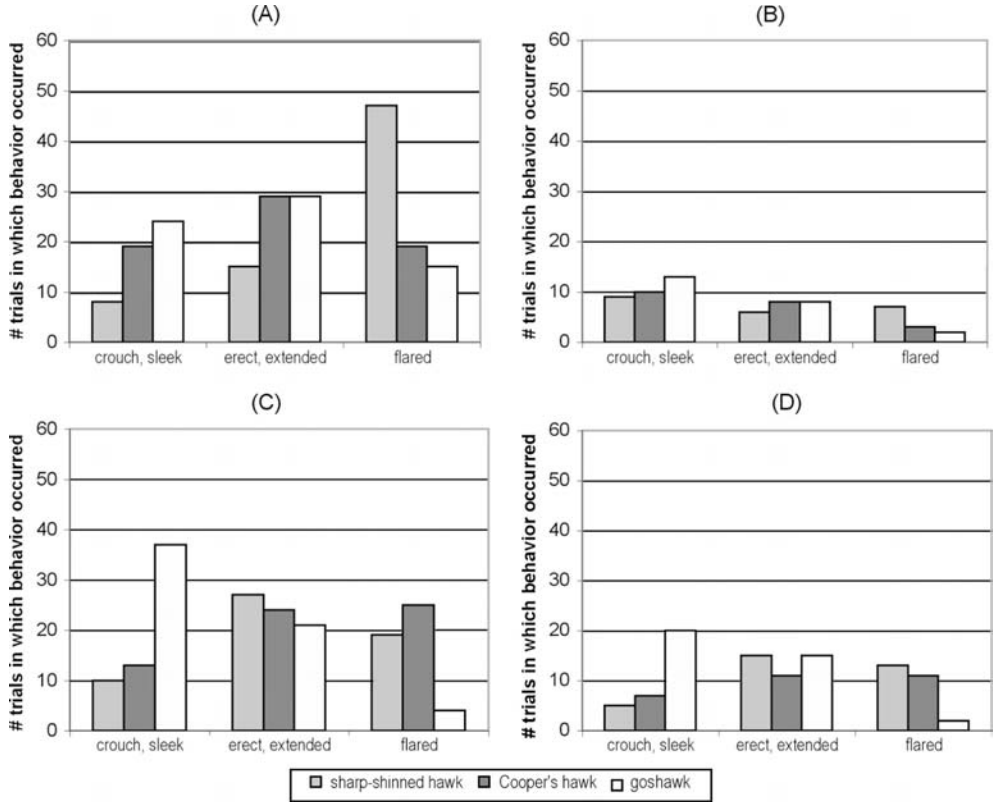

Fig. 3 Chicken anti-predator responses. Non-vocal responses in the brood and non-broody phase: (**a**) female postures: trials 1–9, broody (0–1 min, n=9); (**b**) female postures: trials 10–15, non-broody (0–1 min, n=9); (**c**) male postures: trials 1–9, broody (0–1 min, n=9); (**d**) male postures: trials 10–15, non-broody (0–1 min, n=9)

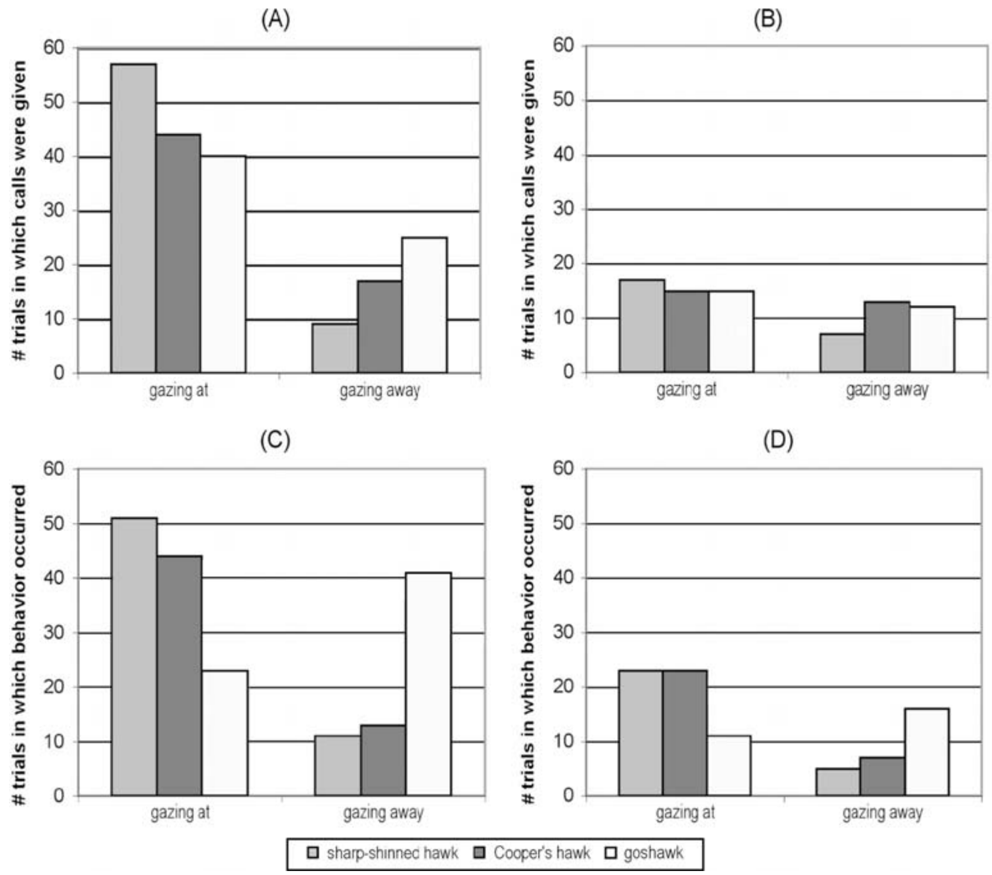

Fig. 4 Chicken anti-predator responses. Non-vocal responses during the broody and non-broody phase: (**a**) female gaze: trials 1–9, broody (0–1 min, n=9); (**b**) female gaze: trials 10–15, non-broody (0–1 min, n=9); (**c**) male gaze: trials 1–9, broody (0–1 min, n=9); (**d**) male gaze: trials 10–15, non-broody (0–1 min, n=9)

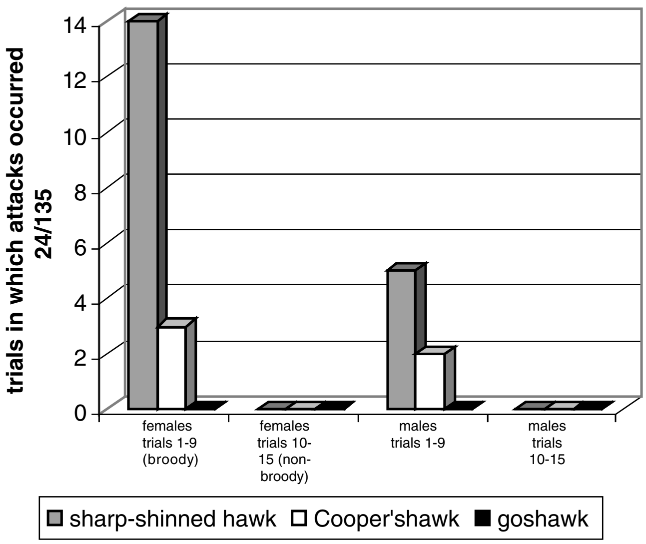

Fig. 5 Attacks (fast running or flying approaches toward the predator), n=9

no significant change in vocal and non-vocal measures and propensity to attack within trials 1–9.

Male non-vocal responses in the "broody" and "non-broody" phases differed from those of females in interesting ways. They also provide an important control for the "broody"–"non-broody" comparison. If the changes in female responses were simply the result of habituation with repeated testing, male responses should change in a similar fashion. In fact, when factored for trial order, males showed no change, behaving similarly throughout the experiment. They showed no significant change in posture or gaze direction (Figs. 3c, d and 4c, d) as the experiment progressed. The likelihood of attack did decrease as the experiment progressed, as the broody period came to an end, and the young matured (Fig. 5). However, even during the broody phase, males attacked much less often than females. When they did so, females invariably initiated the attacks, with males attacking moments later. Thus it appears that females are primarily responsible for the distinctive responses seen during the broody phase.

Vocal responses to the three hawks

When we pool the data, we find statistically significant differences in responses of both sexes to the three hawks, in flight and perched (Table 1). In pair-wise comparisons, responses to the small hawk compared with those to the medium hawk were significantly different (Table 2). When the small hawk was compared to the large hawk there were also marked differences in alarm calling behavior. More aerial alarm calls were given to the large hawk and more ground alarm calls were given to the small hawk. Vocal responses to the medium hawk and large hawk were not significantly different (Table 2).

Separating vocal responses of the two sexes to hawks in flight, those of females differed significantly in call type, between the small hawk and the medium hawk as well as between the small hawk and the large hawk. They gave more aerial alarm calls to the large hawk than to the small hawk. As already noted, aerial alarm calls are present in the female repertoire only when they are broody. The ground predator alarm call is given at all times. Female vocal responses did not differ significantly between the medium hawk and the large hawk in flight. They gave more ground alarm calls than males (75%) to hawks overall, but especially during the flying phase of each test. On the rare occasions when males gave a ground alarm call to a flying hawk, the female gave ground alarm calls before the male.

Males also gave qualitatively different vocal responses to the three hawks in flight. Between the small hawk and the medium hawk in flight there was a significant difference through all 15 trials. Differences in vocal responses between the small hawk and the large hawk and also between the medium hawk and the large hawk were also significant. Males gave relatively more aerial alarm calls and fewer ground alarm calls to the larger hawks, and more ground alarm calls and fewer aerial alarm calls to the smaller hawks.

Considering all trials, female responses differed between the three perched hawks (Table 1). They gave more ground alarm calls and fewer aerial alarm calls to the perched small hawk as compared to the medium and large hawks, but with no differences between the latter two. Like females, males also called differently in response to the three perched hawks (Table 1). As with hawks in flight, males gave more alarms to the larger hawk, including more aerial alarm calls and fewer ground alarm calls. For both sexes, the smaller the hawk, the fewer the number of aerial alarm calls and the greater the number of ground alarm calls.

Comparisons of vocal responses in the "broody" and "non-broody" stages are revealing. Combining the perched and flight phases, and focusing explicitly on the broody stage (trials 1–9), females gave significantly more aerial alarm calls to the medium and large hawks than to the small hawk (Fig. 6a). Later, however, when the chicks were more than 3 weeks of age, aerial alarm calling declined drastically (Fig. 6b). At this stage, only three aerial alarm calls were given by females. All were in the fourth week, with none in the fifth week, confirming that female aerial alarm calling is largely restricted to the broody phase. By comparison, there were 51 calls during the first 3 weeks in trials 1–9. Subsequently, when they gave alarm calls at all, females gave only ground alarm calls. This decrease in aerial alarm call use over time had the overall consequence that females were more likely to ground alarm call to flying hawks than males. When the results were factored by trial, females showed an increasing trend to refrain from alarm calling as the experiment progressed and the chicks grew older. In contrast, male vocal behavior did not change significantly during the "broody" and "non-broody" stages. Unlike females, males showed no significant decrease in aerial alarm calling throughout the experiment, and no increase in the number of trials in which there was no calling (Fig. 6c, d). Apart from the occasional attacks on the predator in the broody phase, usually initiated by the female,

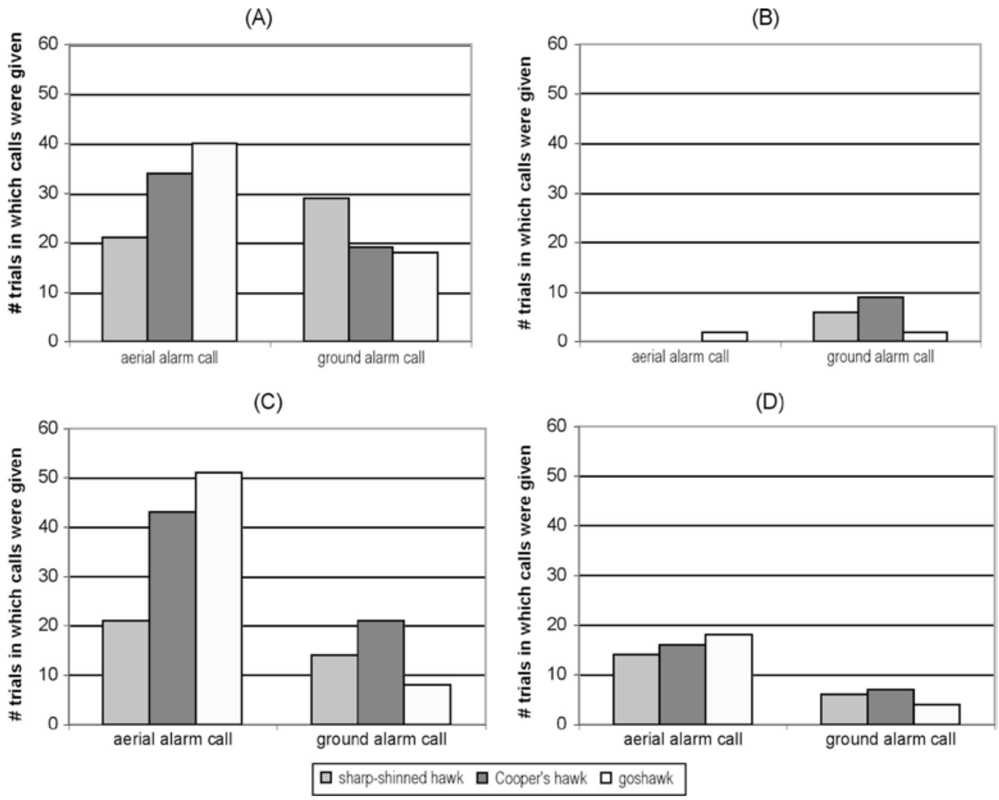

Fig. 6 Chicken anti-predator responses. Vocal responses in the broody and non-broody phase: (**a**) female vocalizations: trials 1–9, broody (0–1 min, n=9); (**b**) female vocalizations: trials 10–15, non-broody (0–1 min, n=9); (**c**) male vocalizations: trials 1–9, broody (0–1 min, n=9); (**d**) male vocalizations: trials 10–15, non-broody (0–1 min, n=9)

males showed none of the changes that females displayed as the experiment progressed and the chicks grew older (Fig. 6).

To summarize, whether the hawks were perched or in flight, both males and females responded very differently to the three accipiter species. In response to the largest hawk, the goshawk, adult chickens of both sexes tended to crouch and sleek, to look away, and to give aerial alarm calls. In response to the smallest raptor, the sharp-shinned hawk, they tended to look towards the predator with an upright, often ruffled posture and were more likely to give ground alarm calls, and to attack. Males, but not females, responded differently to the medium sized Cooper's hawk when compared to the large goshawk. Females reacted much more strongly in the broody phase, attacking the hawks frequently, especially the small sharp-shinned hawk, with aerial alarm calling restricted to this phase. As they ceased to be broody, females refrained from attacking, alarm called much less, and gave only ground alarm calls, especially to the sharp-shinned hawk.

Discussion

This study was designed to examine the degree to which prey species make within predator-class discriminations, and whether such discriminations can be related to vulnerability. We focused specifically on the domestic chicken's capacity to discriminate among raptors differing in size relative to their prey, and thus in the potential threat they represent. A subsidiary goal was to assess whether trained raptors are of value as eliciting stimuli in studies of anti-predator responses, and whether the pattern of responses converges or diverges with observations of natural predation events and those simulated with models or video in the lab.

Trained raptors clearly represent effective stimuli for studies of anti-predator behavior in domestic chickens and, most likely, galliforms more generally. Depending on the condition, chickens displayed species-typical anti-predator responses to the three trained raptors. Moreover, the methods for training raptors worked well as evinced by the consistency with which each of them performed from test to test. This approach is an important methodological advance for students of behavior interested in the dynamics of predator–prey interactions, allowing for relatively natural encounters, but under controlled conditions.

The results support the hypothesis that galliforms discriminate among raptors that differ in size. We controlled for as many differences between raptors as possible, leaving size as the primary discriminative cue. Galliforms showed highly distinctive responses to the three raptors, varying with parental state. Generalizing, chickens tended to show highly evasive responses to the largest raptor, and more aggressive responses to the smaller raptors. The data suggest that the response of adult chickens is sensitive to the degree of lethal danger either to themselves or their dependent young, paralleling studies of other animals. The behavior may also reflect an appreciation of the potential deterrent value for a bird to attack a predator similar in size to itself compared with a larger one. Whereas the large goshawk represents a considerable threat to adults, as reflected in the size of prey items goshawks typically take, the small sharp-shinned hawk poses almost no threat to adult males, and a minor one to adult females. however, the sharp-shinned hawk presents a serious threat to chicks, as is reflected in the heightened response of adults when young chicks are present. Thus, the results show that domestic chickens make distinctions among raptors, and that relative size represents a critical feature in this discrimination.

In addition to the relationship between raptor and chicken size, the alarm response is further modulated by the parental state of the hen. Broody hens showed distinctive responses to raptors, when predator size was held constant. Specifically, broody hens were more aggressive to raptors than non-broody hens, especially in response to the smaller raptor to which newly hatched young are especially vulnerable. The aerial predator call is only given by females when they are broody.

The results also reveal differences in calling behavior with respect to raptor size. Both males and females gave more aerial predator alarm calls to the large goshawk and more ground predator alarm calls to the smaller sharp-shinned hawk. These data have a bearing on the referential signaling hypothesis (Seyfarth et al. 1980a, b; Marler 1985; Cheney and Seyfarth 1982; Marler et al. 1992; Hauser 1996). We see several views of what alarm calls encode. The first, based on early studies of vervet monkeys (Seyfarth et al. 1980a, b), rhesus macaques (Gouzoules et al. 1985), Diana monkeys (Zuberbühler et al. 1999) and domestic chickens (Marler et al. 1992), suggests that animals have calls that pick out or refer to distinctive objects and events in the environment. An alternative explanation is that animals, including those cited above, have alarm calls that provide information about the location and rate of movement of a predator, but the particular species of predator plays no role. Thus, "aerial" and "ground" may not necessarily refer to the type of predator, but rather to some combination of the nature of the danger and the distance, direction, or location from which the threat appears. Under this description, a raptor can elicit both aerial and ground alarm calls depending upon its relative position. This would account for the elicitation of both aerial and ground alarm calls by raptors in this study. This explanation is incomplete, however, because, with these factors held constant, the frequency of ground versus aerial alarm calls varied as a function of raptor size. Specifically, in these close encounters with raptors, adult male and female chickens both gave more aerial alarm calls to large raptors and more ground alarm calls to small raptors. This pattern suggests a third explanation. If we take the point of view of a listener rather than a caller (Seyfarth and Cheney 2003), signals may be regarded, not as specifying particular predatory species or particular locations, but as Marler (1961) and (Marler et al. 1992) have suggested, as selecting specific classes of response (see also Manser et al. 2001). There is frequently an aggressive component in responses to ground alarm calls, often accompanied by erect postures and alert conspicuous behavior, and it is not uncommon for birds mobbing a predator to attack it, while giving ground predator calls, as described years ago in the chaffinch (*Fringilla coelebs*) (Marler 1956). In the present study, the so-called ground alarm call was most often given to small raptors, species that provide little threat to adult chickens, and adults often followed ground predator alarm calls with an attack on the small raptor. In contrast, aerial predator alarm calls were consistently given to the large goshawk, perched or flying, a species that poses a lethal threat to adults. These calls were associated with cryptic responses, as though seeking to evade detection. This third explanation is the best fit with the data presented although further experiments are clearly needed for a complete understanding, both of what alarm calls encode, and importantly, what others are able to decode from them.

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