Anti-predator behaviour of captive Grey partridges (Perdix perdix)

L. Beani 1 and F. Dessì-Fulgheri 1,2

- ¹ Dipartimento di Biologia Animale e Genetica, Università di Firenze, Via Romana 17, 50125 Firenze, Italy
- ² Centro di Studio per la Faunistica ed Ecologia Tropicali, Consiglio Nazionale delle Ricerche, Via Romana 17, 50125 Firenze, Italy

Accepted 7 April 1998

Different experiments of simulated predators (flights of a raptor model, playbacks of raptor whistles and of alarms by conspecifics) were carried out on groups of captive Grey partridges (*Perdix perdix*) from game-farm stock, either intensively- or parent-reared. Both flights and alarms elicited high levels of antipredator behaviour. Freezing and vigilance occurred significantly more in parent-than in intensively-reared coveys. Upright vigilant posture was performed significantly more by males than by females. Good sentinels, i.e. the more vigilant males, formed a stable pair bond earlier than the other males. Advanced reproductive timing might compensate for the increased risk of predation from a sustained vigilance.

KEY WORDS: Grey partridge (*Perdix perdix*), simulated predator, anti-predator behaviour, rearing modality, sexual dimorphism, pair formation.

Introduction																	185
Materials and	meth	ods															186
Results .																	188
Tests of s	imul	ated	pr	edat	ors	in p	are	nt- a	and	inte	nsiv	ely-	rear	ed c	ove	ys	188
Sexual aı	nd in	divi	lua	l dif	fere	nce	s in	vigi	lanc	e ai	nd c	allir	ıg le	vels			190
Discussion																	192
Acknowledgen	nents																194
References																	195

INTRODUCTION

"Animals survive only by being vigilant for predators. But how can we tell where an animal is looking and what it is looking for? Vigilance in animals is a frustrating thing to study" (LAZARUS 1990). This sentence stresses a critical point of

many studies of anti-predator behaviour, that is the difficulty in defining when an animal is being vigilant. In fact the stimulus, the predator, may not be easily detectable by the researcher in the absence of clear predation attempts or events, which may rarely occur during observations in the field. A way to overcome this problem is to simulate the predator's approach and to record the behavioural responses of animals. "The most direct evidence of any anti-predator strategy" LAZARUS (1990) outlines "is that individuals become more vigilant (freeze, escape and so on) when the risk of predation increases".

In this study of the defensive behaviour of Grey partridges (*Perdix perdix*), the presence of predators was simulated by the use of a small aerial silhouette of a raptor, similar to those employed in the classical experiments of K. Lorenz, N. Tinbergen and others (Schleidt 1961), and by playbacks of both calls of raptors and alarms by conspecifics towards aerial predators. Repeated trials of simulated predators were conducted on groups of partridges, both intensively- and parent-reared, during the gregarious phase. In winter, Grey partridges live in coveys, formed by one or more families and by unsuccessful breeders (Jenkins 1961, Cramp & Simmons 1980, Potts 1986, Birkan & Jacob 1988). Coveys split off as a consequence of pair formation, which occurs both within and among winter flocks from the end of January through March, depending on the photoperiod, temperature and weather conditions (Blank & Ash 1956, Weigand 1980, Birkan & Jacob 1988).

The aims of this study were: first, to test the effectiveness of a set of stimuli (flights and whistles of raptors, alarms by conspecifics) and to quantify the defensive response of Grey partridges under controlled conditions; second, to evaluate the influence of rearing modality on the anti-predator behaviour of captive partridges tested in stable groups; third, to compare the individual behaviour of birds a few seconds after the disappearance of the raptor model or after the end of the playback. We wished to investigate whether sexual dimorphism and "sentinel" roles exist in the coveys, and whether guard calling behaviour may affect pair formation, according to the results of mate choice trials in the arena focused on vigilance (Dahlgren 1990) and other behavioural traits (Beani & Dessì-Fulgheri 1995).

MATERIALS AND METHODS

Animals

We conducted our research on yearling Grey partridges, hatched in July, from a commercial game-farm stock (Allevamento Provinciale Torre Certalda, Perugia). We set up two types of experimental groups:

- 1. "Parent-reared coveys" (n=2). Eighteen (8 males and 10 females) and 24 (12 males and 12 females) individuals from two or more parent-reared broods (raised by their parents) which were hatched in an incubator and paired after free mate choice. They were bred in small outside pens and housed together without adults at the age of about 3 months after 1 week spent in visual contact through a mesh-screen.
- 2. "Intensively-reared coveys" (n = 2). Birds reared in brooder houses, allowed into outside pens at 3 weeks of age in stable groups of 30 (15 males and 15 females) and 29 subjects (14 males and 15 females).

The different group size between coveys of type 1 and 2 depended on a higher mortality rate in parent- than in intensively-reared coveys. Our experimental groups were rather large

(in the field a covey ranges from 5 to 25 birds, see Cramp & Simmons 1980), in order to ascertain the behaviour of birds released in large groups, about 25-35 animals.

Male and female partridges were wintered together inside four $50~\text{m}^2$ enclosures on grass, equivalent with regard to their vegetation cover (scattered tufts of grass, 20-30~cm high), provided with mangers, shelters and sand for dusting. Birds were individually marked by coloured plastic rings on their legs.

Test apparatus and procedure

Parent- and intensively-reared coveys were exposed to three types of predatory stimulus, on 12 sunny days between mid-December and January. Birds were 6-7 months old. We combined two or three different trials on each test days.

- (a) 'Flying' buzzard-like silhouette (n = 6 trials per group). A black wooden model of *Buteo buteo* (a natural predator of partridges, see BIRKAN & JACOB 1988) with a wingspread of 15 cm, was pulled by an electric motor at the speed of 1.9 m/sec at 3 m above the ground (for a similar apparatus, see GYGER et al. 1986). This fast-moving stimulus, with an apparent speed of 12.6 body lengths/sec, is more effective than slower stimuli in eliciting anti-predator behaviour (EVANS et al. 1993). This apparatus mimicked a raptor with a wingspread of 100 cm, flying at a speed of approximately 45 km/hr at 20 m above the ground.
- (b) Playback of whistles of raptors (n = 12 trials per group, 6 for each raptor type). Two 15-sec bouts of whistles were broadcast through a loudspeaker adjacent to one side of the enclosure. To avoid the rapid response habituation associated with the repeated presentation of an identical stimulus, whistles of different natural predators of partridges (POTTS 1986) were produced (6 *pi-uu* notes of the buzzard, *Buteo buteo*, and 9 *kak* notes of the goshawks, *Accipiter gentilis*; PETERSON et al. 1983). Four bouts of calls, two for each type, were alternately presented on the same day, at intervals of 30 min or more.
- (c) Playback of alarms by conspecifics (n = 12 trials per group). Two 10-sec natural bouts of 4 notes were presented to the same covey during each test day at intervals of 2 hr at least. Grey partridges give qualitatively different vocalizations in response to aerial and terrestrial predators. Alarms towards raptors ("aerial predator calls", McCabe & Hawkins 1946, Lynn-Allen & Robertson 1956, Birkan & Jacob 1988; in terms of elicited reaction, "squatting notes", Dessì-Fulgheri et al. 1986) consist of an harmonic low-frequency note, uttered 1-4 times (see the sonogram in Dessì-Fulgheri et al. 1986), typically in the presence of aerial predators or when the source of danger is unclear.

Moreover, we recorded the behavioural responses to natural predators, mostly corvids, passing over the aviaries. Reactions to 24 and 11 flights were observed, respectively, in intensively- and parent-reared coveys.

Behavioural records and statistical analysis

The behavioural responses of birds to the stimuli were divided into four mutually exclusive categories and were recorded during the presentation of the stimulus, and 30 and 60 sec after its disappearance:

- 1. Vigilance: outstretched neck, upright posture, and movements of the head, i.e. scanning from side to side (since birds, unlike mammals, can only move their eyes a little within the skull, movements of the head are good indicators of eye movements, and far easier to monitor; see LAZARUS 1990).
- 2. Freezing/crouching: the bird remains motionless, sometimes after a rapid squatting on the ground.
 - 3. Escape: running towards vegetation cover and hiding.
- 4. Non-anti-predator behaviour: any behaviour not falling into one of the above categories.

Since group size was different, behavioural records of coveys were represented as absolute percentages of birds performing mutually exclusive behaviours (see stacked bars of Fig. 1) in 6, 12 and 12 trials of the a, b and c stimulus types, respectively. Because the data were collected as the proportions of birds behaving in a certain way at each trial (considered as repetitions of the a, b and c tests), data were transformed [arcsin (x)] in order to perform an analysis of variance on the entire set of group responses. A repeated-measures ANOVA [A factor: rearing modality (2 levels, 2 groups \times each level). B factor: repeated trials (6 or 12)] was conducted to evaluate differences due to rearing modality, intra-group variability and repeated trials. A one-factor ANOVA [stimulus type (2 or 3 levels)] was performed when appropriate, i.e. in the absence of any significant difference between groups and repeated trials. All statistical comparisons were two-tailed, with an alpha level of 0.05.

Individual vigilance levels and calling performance in both parent- and intensively-reared coveys were computed from 30 trials of the a, b, c simulated predators. The subject in an upright alert posture 30 sec after the visual or acoustic stimulus (or uttering one or more calls in the min following the stimulus) scored 1, while the score was 0 in all other cases; vigilance and calling scores ranged from 0 to 30. Whereas warning calls were typically accompanied by a crouching posture, the so-called "rusty-gate calls" — the commonest vocalization during the gregarious period, frequently given after covey break-up (McCabe & Hawkins 1946, Dessì-Fulcheri et al. 1986, Fusani et al. 1994) — were uttered in an upright posture and thus were individually measurable.

To investigate pair formation within each experimental covey, three 10-min observations per day were carried out on 16 different dates between 2 December and 3 March, at intervals of 6-8 days. Two individuals were considered to be forming a stable pair at a certain date if they were clearly synchronized and spaced from the covey and they performed mate guarding, reciprocal courtship and/or copulations during all the observation sessions of that day (for details, see Beani et al. 1988). Subsequent observations confirmed the consistency of the assigned pair bond. Males without a stable pair bond at the last observations (n = 7) were allowed into a pen with 10 "naïve" females, that is never seen before by males; since they all paired within the next 3 days, we considered these individuals as paired at the 16th observation day. Pairing score ranged from 1 (early pair) to 16 (late pair), depending on the date of pair formation. Vigilance and calling scores between sexes and rearing type, and the relationship between pairing scores and either vigilance or calling scores, were evaluated by means of nonparametric statistics (Mann-Whitney U test; Spearman rank correlation coefficient; Siegel 1956).

RESULTS

Tests of simulated predators in parent- and intensively-reared coveys

The responses of the Grey partridges to the raptor model are shown in Fig. 1A. The rates of freezing during the passage of the raptor silhouette (Repeated-measures ANOVA, df = 1,5,17. Rearing type factor: F = 24.97, P < 0.03. Repeated-measures factor: NS. Interaction: NS), and 30 sec after its disappearance (Rearing type factor: F = 35.89, P < 0.02), were significantly higher in parent- than in intensively-reared coveys, which consequently exhibited significantly higher rates of non-anti-predator behaviour at both samplings (Rearing type factor: F = 72.2, P < 0.01; F = 29.38, P < 0.03). These differences had disappeared after 60 sec, when almost all birds were engaging in non-anti-predator behaviour. There was no difference between subsequent trials: repeated-measures factors and interactions were never significant in the entire data set.

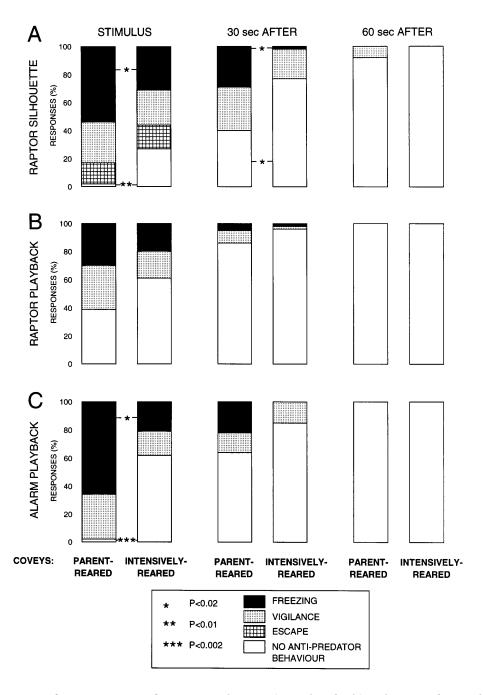


Fig. 1. — Defensive responses of parent-reared coveys (18 and 24 birds) and intensively-reared coveys (29 and 30 birds) of Grey partridges to different stimuli: (A) raptor silhouette (6 trials × group); (B) playback of raptor whistles (12 trials × group); (C) playback of alarms by conspecifics (12 trials × group). Values shown are absolute percentages of birds performing mutually exclusive behaviours.

A similar trend was observed during sporadic flights of corvids, kestrels and buzzards over the aviaries (freezing on encountering raptors: 86% in parent- vs 48% in intensively-reared coveys, during respectively 11 and 20 natural flights over the aviaries). Contact calls stopped during both simulated and true raptor flights, and resumed more quickly in intensively- than in parent-reared coveys (respectively, after 30 and 60 sec from the flight in 90% of the trials). After a silent pause, the first rusty-gate call typically elicited a movement towards the manger; it was uttered sooner in intensively- than in parent-reared coveys: 18 vs 38 sec after the passage of the raptor model (one-factor ANOVA. Rearing type factor: F = 10.71, df = 1,22, P < 0.005), 20 vs 43 sec after the true raptor flight (F = 7.26, df = 1,33, P < 0.01).

Responses of Grey partridges to playbacks of raptor calls are shown in Fig. 1B. Reactions to the whistles of the goshawk and buzzard have been lumped together, since there was no significant difference between them (one-factor ANOVA, df = 1,22. Goshawk vs buzzard whistles in parent- and intensively-reared coveys, respectively: freezing, F = 1.9 and 0.19; vigilance, F = 0.32 and 1.55; non-anti-predator behaviour, F = 1.61 and 1.8; NS). Although birds in parent-reared coveys were motionless and vigilant more than the others during the acoustic stimulus, these differences were never significant (Repeated-measures ANOVA, df = 1,11,35. Rearing type factor: 30 vs 20% of freezing, F = 0.2, NS; 31 vs 19% of vigilance, F = 10, P = 0.08). Behavioural responses did not change between different playback tests (Repeated-measures factor: NS for all the behaviours). Recovery time was short in all groups. Thirty seconds after the stimulus no defensive reaction was recorded in about 90% of the trials. The first rusty-gate call occurred 18 and 23 sec after the playback, respectively, in parent- and intensively-reared coveys.

Playbacks of alarms by conspecifics were effective in eliciting a defensive response (Fig. 1C). During the stimulus, there were significantly higher levels of freezing (66 vs 21%) in parent- than in intensively-reared coveys (Repeated-measures ANOVA, df = 1,11,35. Rearing type factor: F = 36.85, P < 0.02). Birds in the intensively-reared coveys returned to non-frightened activities still during the playback (F = 487.06, P < 0.002). The timing of the first call was 29 sec after the end of the stimulus in parent-reared coveys, 28 sec in intensively-reared ones.

A comparison between the three danger simulations revealed a different degree of response to the three stimuli, the whistles of raptors being the least effective. The frequency of non-anti-predator behaviours was lower during the passage of the silhouette and the alarms than during the whistles both in parent- (one-factor ANOVA, df = 2,57; F = 21.02, P < 0.001) and intensively-reared coveys (F = 6.83, P < 0.002). Freezing occurred more often in the silhouette and alarm trials than in the whistle tests (significantly in parent-reared coveys: F = 13.9, P < 0.001), whereas the rate of vigilance was not affected by the type of stimulus. Thirty seconds after the stimulus, there were significant differences regardless of rearing modality; the raptor whistles were the weakest stimulus whereas the silhouette was the strongest (non-anti-predator behaviour in parent- and intensively-reared coveys, respectively: F = 12.69, P < 0.001 and F = 4.01, P < 0.02; vigilance: F = 6.63, P < 0.003 and F = 5.31, P < 0.01).

Sexual and individual differences in vigilance and calling levels

With regard to individual behaviour, guards were non-randomly distributed in the covey. Some individuals tended to be more vigilant than the others and more

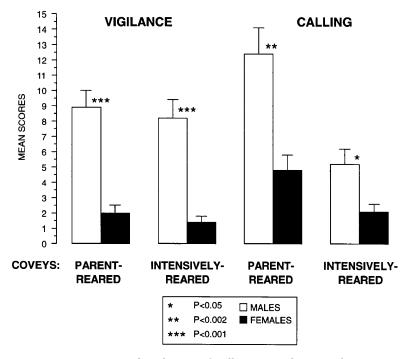


Fig. 2. — Comparison of vigilance and calling scores between the sexes in parent- and intensively-reared coveys of Grey partridges after simulated predatory encounters (alarm calls, predator calls and raptor models). Values shown are mean scores (\pm SE).

prompt to utter the first rusty-gate call after the silent pause. For this analysis, we lumped together the reactions to the different simulated predators (flights of silhouettes, playbacks of whistles and of alarms: Fig. 2), because all these stimuli were effective. The alert upright posture was more frequently assumed by males than by females in both parent- (U = 31.5, z = 4.2; N_1 = 20, N_2 = 22; P < 0.001) and intensively-reared coveys (U = 100, z = 5.1; N_1 = 29, N_2 = 30; P < 0.001). Clear sexual dimorphism was also found in the number of calling birds 30 sec after the stimulus; most callers were males, both in parent- (U = 66.5, z = 3.1; P < 0.002) and intensively-reared coveys (U = 309, z = 1.9; P < 0.05). Moreover, the number of callers was significantly higher in parent- than in intensively-reared coveys both for males (U = 133.5, z = 3.1; N_1 = 29, N_2 = 30; P < 0.002) and for females (U = 162.5, z = 2; N_1 = 22, N_2 = 30; P < 0.03), whereas there was no significant difference in the alert posture between rearing types.

Vigilance and calling scores were positively correlated in males (n = 49, r_s = 0.56, P < 0.01): good sentinels were also good callers. Regardless of rearing type, a significant negative correlation (Fig. 3) was found between the dates of pair formation during the observation period and male vigilance scores (n = 49, r_s = – 0.68, P < 0.01). Similarly, calling score was negatively correlated to pairing dates in both parent- (n = 20, r_s = – 0.53, P < 0.01) and intensively-reared coveys (n = 29, r_s = – 0.60, P < 0.01): sentinels and callers formed a stable pair bond earlier than the others.

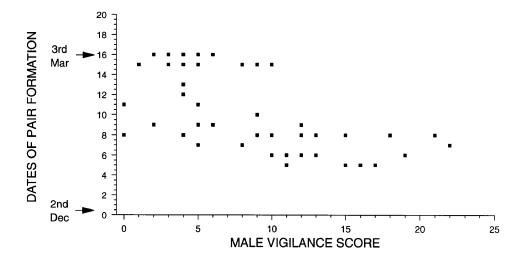


Fig. 3. — Dates of pair formation and vigilance scores of 49 males in parent- and intensively-reared coveys. First-pairing males were good sentinels ($r_s = -0.68$, P < 0.01).

DISCUSSION

The classical experiments with flying-hawk models were recently reviewed (CANTY & GOULD 1995) and redesigned by means of computer-generated animations (EVANS et al. 1993). The high rate of responses generated by a raptor silhouette moving overhead and by playbacks of raptor whistles or conspecific alarm, encouraged us to adopt a simple and traditional apparatus, in order to test groups of Grey partridges in semi-natural conditions.

A first advantage of the techniques of the simulated predator is the large sample of behavioural records generated; to avoid habituation (e.g. HIRSCH et al. 1955, MELZACK 1961, MELVIN & CLOAR 1969), stimuli have to be varied and trials highly spaced, as in our experiment. A second advantage is the possibility of testing antipredator behaviour by means of repeatable visual or acoustic stimuli, in a definite space (here, large grassy enclosures without objects that might obscure a predator's approach) and on selected groups of marked individuals. Thus, we controlled for the following variables: distance, speed and type of predator; cover degree, a factor deeply affecting both predator's detection and behavioural response; group size; group composition, in order to avoid any possible "audience effect" (see GYGER et al. 1986, KARAKASHIAN et al. 1988). A third advantage is the effectiveness of rough raptor models in eliciting peculiar behavioural responses by galliforms. Current evidence suggests that, unlike some mammals (e.g. vervet monkeys Cercopithecus aethiops, SEYFARTH & CHENEY 1986) and birds (lapwings Vanellus, Walters 1990), the expression of anti-predator behaviour in galliforms is not principally dependent on the fine structure of objects (see Schleidt 1961 for the response of turkeys Meleagris gallopavo to models greately differing in their apparent size and speed; see also GYGER et al. 1987, for the alarms elicited in chickens by a broad array of airborne objects).

An overall view of the behavioural responses of partridges (Fig. 1) reveals that an overflying silhouette of a buzzard, repetitions of whistles of raptors and alarm calls were all able to elicit a definite reaction. The defensive behavioural repertoire described in the field (McCabe & Hawkins 1946, Jenkins 1961, Birkan & Jacob 1988) agrees with our records from birds in large enclosures. At least in the commercial stock tested in this study, the domestication process (the partridge has been subjected to intensive hand rearing in the last 30 years) has not deeply altered the anti-predator behaviour. The rather low rate of escape (see Fig. 1) could be due to the scarcity of cover in our aviaries. Freezing followed by sustained vigilance may represent an effective strategy towards aerial predators in open country, combining camouflage and detection of the predator. Our partridges, mainly parent-reared birds, showed a strong response to the silhouette and to alarm calls (Fig. 1A, C), whereas the whistles of a raptor out of view represented a less potentially dangerous situation and elicited a relatively short reaction (Fig. 1B). Moreover, raptors are usually silent during hunting.

With regard to the influence of rearing modality, there are two main sources of variability among groups: first, the presence of parents during the first weeks of life (i.e. a different imprinting process); second, early or late experience of approaches by natural predators, depending on outside housing. Therefore we are comparing the effects of a complex of variables. Freezing and crouching were more often performed by parent-reared partridges, and usually a few seconds after the raptor had disappeared, whereas many intensively reared birds were vigilant in an upright posture and returned to common activities sooner (Fig. 1A). A similar response was observed in the playback trials (Fig. 1B, C). Fine tuning of antipredator responses is influenced by rearing methods. Although anti-predator behaviour in galliforms is inherited, partridge chicks learn to direct the most suitable behaviour against specific predators from their parents.

These data agree with the results of similar experiments conducted on Grey partridges and pheasants (Dowell 1990, 1992) and Red-legged partridges (ZILLETTI et al. 1993), and with a recent study carried out in Finland on wild, parent- and hand-reared chicks of Grey partridges (ANTTILA et al. 1995). The latter study showed a certain degree of variation in anti-predator behaviour between parent-reared broods, suggesting that the quality of the parents may also be important. Our experimental design did not consider this critical component, because our parentreared coveys were formed from different broods; moreover, the age of the birds (chicks vs subadults) and the testing modality (isolated vs 20-30 birds together) were different between ANTTILA's study and ours. The covey, the gregarious unit characteristic of partridges, may be a critical component of their defensive strategy in the wild. Unpaired males suffer higher rates of mortality than paired ones and are more vulnerable to raptor predation (Potts 1980); this perhaps applies to isolated partridges throughout the year. In Grey partridges, behaviour is highly synchronized, especially within familial units; the higher frequency of rusty-gate calls in parent- than intensively-reared coveys is consistent with a well integrated social system (Fig. 2). Therefore our tests were conducted on heterosexual groups in late winter, when gregariousness is combined with pair formation. The evaluation of pairing success in groups previously studied with regard to their defensive behaviour has been conducted only in this experiment.

A few sentinels are able to alert large flocks (Beani & Dessì-Fulgheri 1986). Vigilance and calling behaviours were typically performed by males, regardless of rearing type (Fig. 2), and mainly by the individuals with early formation of a stable

pair bond (P < 0.01). Sexual dimorphism in vigilance agrees with the results of the study conducted by Dahlgren (1990) in the field during the pre- and post-hatching period, and with our previous observations in captivity (Beani & Dessì-Fulgheri 1984). In this species testosterone levels affect vigilance: testosterone-implanted males are more vigilant than controls (Fusani et al. 1997). A similar sexual asymmetry in sentinel behaviour was found in the Florida scrub jay ($Aphelcoma\ c.\ coerulescens$), though age is a stronger determinant of vigilance than sex in this gregarious species with cooperative breeding (Hailman et al. 1994). Short-term trials of mate choice (Dahlgren 1990; Beani & Dessì-Fulgheri 1994, 1995) confirm the critical role of both vigilance and vocal performance in the selection of a mate by female partridges.

Although alertness itself enhances individual survival, a partridge in the upright guard or calling posture is more easily detected by an aerial predator; in a study carried out in North Dakota (Carroll 1990), the higher survival rate of females than of males (59% vs 19%) has been explained by behavioural differences between the sexes. Moreover, vigilance is probably conducted at the expense of foraging time (Dahlgren 1990). The cost of these conspicuous male behaviours could be compensated by early pairing and high reproductive success. In partridges, to be a sentinel and a caller could be a type of male self-advertisement. In agreement with this hypothesis, Zahavi (1990) treated sentinel behaviour in Arabian babblers (*Turdoides squamiceps*) as a display by which group members could show their status. Sentinel activity could function as an advertisement (Zahavi 1977) and could be a component of female choice of a mate. Nevertheless, a positive relationship between vigilance and pairing was not confirmed in the red-winged blackbird, *Agelaius phoenicus* (Yasukawa et al. 1992).

In conclusion, the anti-predator behaviour of partridges seems to be subtly modulated, changing in relation to the type of stimulus, the type of rearing, and the sex of the birds. Inappropriate anti-predator response is a serious constraint to restocking and reintroduction success in areas, like in Italy, where it may be necessary to employ hand-reared birds, due to the serious decline of the parent-reared populations. The release of familial units, or at least intensively-reared coveys selected for appropriate anti-predator behaviour, could be an alternative to massive releases of intensively-reared young in autumn. Moreover, domestication favours individuals with a high reproductive rate and excludes any selection against wrong defensive responses. The allowance of a certain degree of free mate choice in gamefarm stocks, combined with a "predator training period" before the release (e.g. the experiments on *Colinus viginianus*, Ellis & Serafin 1976) could be a reasonable compromise which would lead to the raising of high-quality birds (Beani & Dessì-Fulgheri 1992).

ACKNOWLEDGEMENTS

This research was made possible by funding from Provincia di Perugia and by the collaboration of the game farm "Allevamento Provinciale di Torre Certalda" (Perugia). This research was also supported by European Union (grant ERBCHRXCT 940472), Ministero dell'Università e della Ricerca Scientifica e Tecnologica (60 and 40%) and "Centro di Studio per la Faunistica ed Ecologia Tropicali" of the Consiglio Nazionale delle Ricerche. We also gratefully acknowledge the help of E. Masi and A. Papeschi during the trials, and of P. Christie for his linguistic revision.

REFERENCES

- Anttila I., Putaala A. & Hissa R. 1995. Tarhattujen ja villien peltopyyn poikasten käyttäytymisestä. *Suomen Riiista* 41: 53-65 (in Finnish).
- Beani L., Cervo R., Lodi L., Lupo C. & Dessì-Fulgheri F. 1988. Circulating levels of sex steroids and socio-sexual behaviour in the grey partridge. *Monitore Zoologico Italiano* (*Nuova Serie*) 22: 145-160.
- BEANI L. & DESSÌ-FULGHERI F. 1984. Leadership and social interactions in a group of Grey Partridges. *Monitore Zoologico Italiano (Nuova Serie)* 18: 159-160.
- BEANI L. & DESSÌ-FULGHERI F. 1986. Gregarious behaviour in a group of captive Grey Partridges (*Perdix perdix*). Bollettino di Zoologia 53: 69-72.
- BEANI L. & DESSì-FULGHERI F. 1992. Influence of mate choice on reproductive success of captive grey partridges (*Perdix perdix*). Gibier Faune Sauvage 9: 729-742.
- BEANI L. & DESSì-FULGHERI F. 1994. Female mate choice in the grey partridge *Perdix perdix*: the role of male vocalizations, p. 414. In: Atti del Convegno Italiano di Ornitologia, Torino 8-11 ottobre 1991. *Torino: Museo Regionale di Scienze Naturali*.
- Beani L. & Dessì-Fulgheri F. 1995. Mate choice in the grey partridge, *Perdix perdix*: role of physical and behavioural male traits. *Animal Behaviour* 49: 347-356.
- BIRKAN M.G. & JACOB M. 1988. La perdix grise. Paris: Hatier.
- BLANK T.H. & ASH J.S. 1956. The concept of territory in the partridge (*Perdix perdix*). *Ibis* 98: 379-389.
- CANTY N. & GOULD J.L. 1995. The hawk/goose experiment: sources of variability. *Animal Behaviour* 50: 1091-1095.
- CARROLL J.P. 1990. Winter and spring survival of radio-tagged gray partridges in North Dakota. *The Journal of Wildlife Management* 54: 657-662.
- CRAMP S. & SIMMONS K.E.L. (Edits) 1980. Handbook of the Birds of Europe, the Middle East and North Africa, Vol. II. The birds of the Western Palearctic. Hawks to Bustards. Oxford: Oxford University Press.
- Dahlgren J. 1990. Females choose vigilant males: an experiment with the monogamous grey partridge, *Perdix perdix*. *Animal Behaviour* 39: 646-651.
- Dessì-Fulgheri F., Beani L. & Piazza R. 1986. Vocalization of the grey partridge, *Perdix perdix* (L.): a spectrographic analysis. *Monitore Zoologico Italiano (Nuova Serie)* 20: 441-458.
- Dowell S.D. 1990. The development of anti-predator responses in grey partridges and common pheasant, pp. 193-199. In: Hill D.A. et al., Edits. Pheasants of Asia 1989. *Reading, UK: World Pheasant Association*.
- Dowell S.D. 1992. Problems and pitfalls of gamebird reintroduction and restocking: an overview. *Gibier Faune Sauvage* 9: 773-780.
- ELLIS D.H. & SERAFIN J.A. 1976. A research programme for the endangered masked bobwhite. *Journal of the World Pheasant Association* 2: 16-33.
- EVANS C.S., MACEDONIA J.M. & MARLER P. 1993. Effects of apparent size and speed on the response of chickens, *Gallus gallus*, to computer-generated simulations of aerialpredators. *Animal Behaviour* 46: 1-11.
- Fusani L., Beani L. & Dessì-Fulgheri F. 1994. Seasonal individual changes in Grey Partridge Perdix perdix male call, pp. 173-181. In: Atti del Convegno Italiano di Ornitologia, Torino 8-11 ottobre 1991. Torino: Museo Regionale di Scienze Naturali.
- Fusani L., Beani L., Lupo C. & Dessì-Fulgheri F. 1997. Sexually selected vigilance behaviour of the grey partridge is affected by plasma androgen levels. *Animal Behaviour* 54: 1013-1018.
- Gyger M., Marakashian S. & Marler P. 1986. Avian alarm calling: is there an audience effect? *Animal Behaviour* 34: 1570-1572.
- Gyger M., Marler P. & Pickert R. 1987. Semantics of an avian alarm call system: the male domestic fowl, *Gallus domesticus*. *Behaviour* 102: 15-40.
- HAILMAN J.P., McGowan K.J. & Woolfenden G.E. 1994. Role of helpers in the sentinel behaviour of the Florida scrub jay (*Aphelcoma c. coerulescens*). Ethology 97: 119-140.

- HIRSCH J., LINDLEY R.H. & TOLMAN E.C. 1955. An experimental test of an alleged innate sign stimulus. *Journal of Comparative Physiology & Psychology* 48: 278-280.
- JENKINS D. 1961. Social behaviour in the partridge (Perdix perdix). Ibis 103a: 155-189.
- KARAKASHIAN S.J., GYGER M. & MARLER P. 1988. Audience effects on alarm calling in chickens (Gallus gallus). Journal of Comparative Psychology 102: 129-135.
- LAZARUS J. 1990. Looking for trouble. New Scientist 27 January: 62-65.
- LYNN-ALLEN E.H. & ROBERTSON A.W.P. 1956. A partridge year. London: Geoffry Bles.
- McCabe R.A. & Hawkins A.S. 1946. The Hungarian partridge in Wisconsin. *The American Midland Naturalist* 36: 1-75.
- MELVIN K.B. & CLOAR F.T. 1969. Habituation of responses of quail, *Colinus virginianus*, to a hawk, *Buteo swainsoni*: measurement through an 'innate suppression' technique. *Animal Behaviour* 17: 468-473.
- MELZACK R. 1961. On the survival of mallard ducks after 'habituation' to the hawk-shaped figure. *Behaviour* 17: 9-16.
- Peterson R., Mountfort G. & Hollom P.A.D. 1983. A field guide to the birds of Great Britain and Europe. *London: Collins*.
- POTTS G.R. 1980. The effects of modern agriculture, nest predation and game management on the population ecology of partridges (*Perdix perdix* and *Alectoris rufa*). *Advances in Ecological Research* 11: 1-79.
- POTTS G.R. 1986. The Partridge. Pesticides, predation and conservation. London: Collins.
- SEYFARTH R.M. & CHENEY D. 1986. Vocal development in vervet monkeys. *Animal Behaviour* 34: 1640-1658.
- Schleidt W.M. 1961. Reaktionen von Truthühnern auf fliegende Raubvögel und Versuche zur Analyse ihrer AAM's. Zeitschrift für Tierpsychologie 18: 534-560.
- SIEGEL S. 1956. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill.
- Walters J.R. 1990. Anti-predator behavior of lapwings: field evidence of discriminative abilities. *The Wilson Bullettin* 102: 49-70.
- WEIGAND J.P. 1980. Ecology of the Hungarian partridge in north-central Montana. Wildlife Monographs 74: 1-106.
- YASUKAWA K., WHITTENBERGER L.K. & NIELSEN T.A. 1992. Anti-predator vigilance in the redwinged blackbird, *Agelaius phoenicus*: do males act as sentinels? *Animal Behaviour* 43: 961-969.
- Zahavi A. 1977. Reliability in communication systems and the evolution of altruism, pp. 253-259. In: Stonehouse B. & Perrins C., Edits. Evolutionary ecology. *Baltimore: University Park Press*.
- Zahavi A. 1990. Arabian Babblers: the quest for social status in a cooperative breeder, pp. 103-130. In: Stacey P.B. & Koenig W.D., Edits. Cooperative breeding in birds: long-term studies of ecology and behavior. *Cambridge: Cambridge University Press*.
- ZILLETTI B., VENTURATO E. & BEANI L. 1993. Comportamento anti-predatorio nella pernice rossa (*Alectoris rufa*): influenza dell'allevamento. *Supplemento Ricerche Biologia della Selvaggina* XXI: 661-667.