

Do northern lapwings *Vanellus vanellus* and little ringed plovers *Charadrius dubius* rely on egg crypsis during incubation?

Miroslav ŠÁLEK¹ and Eva CEPÁKOVÁ²

¹ Department of Ecology and Environment, Faculty of Forestry and Environment, Czech Agricultural University, Kamýcká 129, CZ-165 21 Praha 6, Czech Republic; e-mail: salek@fle.czu.cz

² Agency for Nature Conservation and Landscape Protection, Kališnická 4–6, CZ-130 23 Praha 3, Czech Republic; e-mail: eva_cepakova@nature.cz

Received 13 June 2005; Accepted 19 January 2006

Abstract. We studied the possible role of clutch crypsis in antipredator behaviour in two related species of ground-nesting waders with camouflaged eggs, the northern lapwing (*Vanellus vanellus*) and the little ringed plover (*Charadrius dubius*). We examined whether this behaviour appears regularly in both species and tested the difference in the use of this trait between the two species. The results suggest that both charadriids rely on egg crypsis as a reasonable strategy toward avian nest predators. However, the larger and more conspicuous lapwings use it less frequently than plovers, probably because they rather rely on body size and aggressiveness combined with colonial breeding. Smaller and solitary little ringed plovers tended to hide the nest location more thoroughly than lapwings, probably due to their limited ability to defend the nest actively. Instead of aggressive attacks, they use alternative behavioural elements intended to deceive predators, namely incubation-feigning. Although egg crypsis is regularly used as a passive strategy for protecting nests against predators in both species, it seems to be unprofitable as an exclusive form of nest protection. The birds combine it with other behavioural elements, such as the above mentioned aggressiveness or incubation-feigning.

Key words: antipredator strategies, cryptic coloration, nest predation, escape reaction

Introduction

Waders, as typical ground-nesting birds inhabiting open landscapes, are exposed to high risk of nest predation (Martin 1993, Yanes & Suarez 1995, Jimenez & Conover 2001) and exhibit a variety of antipredator mechanisms using a range of morphological and behavioural traits. To avoid visual detection, many waders, like other birds camouflaged by plumage, crouch tight at the nest and rely on body crypsis combined with vegetation cover, if present (Crampton 1990, Haskell 1996, Lloyd et al. 2000, Albrecht & Klvaná 2004). Other behavioural mechanisms include an active search for a safer nest-site (Lauro & Nol 1995, Solis & Delope 1995, Whittingham et al. 2002, Thyen & Exo 2005) or attacks on predators entering the nesting territories (Larsen & Grundetjern 1997, Schekkerman et al. 1998), combined with colonial breeding (conspecific colonies or associations of several species), which helps to exclude predators more effectively from the breeding sites (Elliot 1985, Crampton 1990, Fitzpatrick & Bouchez 1998, Hegyi & Sasvári 1998, Kis et al. 2000). In general, larger, easily detectable and colonial waders tend to be more aggressive nest defenders than smaller, more camouflaged species that are solitary breeders (Larsen et al. 1996).

Although the use of plumage crypsis and aggressive behaviour close to the nests has been well described in waders, less attention has been paid to antipredator behaviour

*Corresponding author

associated with egg crypsis. The pattern of egg coloration in some birds is considered as an adaptive attribute enhancing camouflage of the clutch against visually-oriented predators (Hockey 1982, Westmoreland & Kiltie 1996, Blanco & Bertellotti 2002, Sanchez et al. 2004), especially in ground-nesting birds (Moreno & Osorno 2003). Since waders possess cryptically pigmented eggs as a rule (Glutz von Blotzheim et al. 1975, Crampton 1990), it might be assumed that prudent leaving of the nest by a parent might be used at least in some less camouflaged species as an alternative to the use of plumage crypsis, i.e. the birds can decide to leave the nest and to rely on the crypsis of their clutch. Corresponding behaviour has been observed in the small and cryptic Temminck's stint (*Calidris temminckii*) by Kovula & Rönkä (1998). South American southern lapwing (*Vanellus chilensis*) also "regularly exhibit early surreptitious departure, quietly running from the nest in a crouched position" (Walters 1990). However, these studies are based on responses of birds to disturbance by humans and thus do not allow a distinction between risk solely for the clutch and risk for the incubating adults themselves. It has yet to be quantified whether waders with camouflage rendered eggs nesting in open habitats with low vegetation cover (e.g. plovers) regularly use egg crypsis as a protective strategy against visually oriented predators of nests. References suggesting the existence of this behavioural trait are episodic and lack quantitative outputs (Crampton 1990).

This study investigates the use of escape behaviour as a response to an approaching nest predator in two related ground-nesting species inhabiting open landscapes – the northern lapwing (*Vanellus vanellus*) and the little ringed plover (*Charadrius dubius*). These two species differ in size, coloration and breeding patterns. The northern lapwing (further referred to as 'lapwing') is a large and conspicuous charadriid with dark iridescent purple-green plumage of hindneck and upperparts. It inhabits a wide range of wetlands, such as fens, bogs and marshes, but also farmland substitutes typically with a sparse mosaic of vegetation producing grey-brown or grey-green tints of the field surface. It may breed solitarily, but loose colonies are preferably established in suitable habitats. The little ringed plover ('plover') is a small wader with dull brown plumage covering most of the upper body parts (nape, back, coverts, tail). As a rule, solitary pairs breed and occupy bare or sparsely vegetated grounds with gravel, shingle or sandy flats on river banks and drained ponds. The nests of both species are shallow scrapes lined with a material from the surroundings, i.e. usually with dry plant stems (lapwing) and small shingles or grit (plover). Lapwing eggs are olive, brown or umber with black spots or streaks. Plover eggs have stone, buff or pale brown ground colour with small dark brown spots and streaks (Glutz von Blotzheim et al. 1975, Crampton 1990, Hudec & Štátný 2005).

The combination of nest lining and dull-pigmented four-egg clutches seem to provide an efficient masking pattern toward visually oriented predators in both species, at least in their commonly used breeding habitats. On the other hand, adults of the two species differ in size and conspicuousness, plovers being smaller and more camouflaged and thus less visible in the field than lapwings. The larger, colonially breeding lapwings are skilled defenders of their nests against predators (Elliot 1985, Kis et al. 2000), though plovers may also use aggressive attacks against various intruders in the nest vicinity (Crampton 1990).

If these open-nesting waders use egg crypsis as a regular response to an approaching visually oriented nest predator, their behavioural repertoire should include the element of passively leaving the nest in the presence of such a predator. Therefore, we firstly examined whether this behaviour appears, as a rule, in both these plovers. Secondly, we tested whether the lapwing uses nest leaving in the presence of a predator more frequently than the plover

because of body conspicuousness or, conversely, less frequently as a result of the use of alternative antipredator strategies such as colonial nesting and aggressiveness.

Study Area

The study was carried out in the České Budějovice (49°15'N, 14°05'E) and Třeboň (49°00'N, 14°45'E) basins, South Bohemia, Czech Republic. Both are flat areas comprising mosaics of cultivated fields and meadows (ca 50 %) and woods (30 %), interspersed with wetlands (15 %), human settlements and roads (5 %). The fields are managed using rotation plans with winter wheat, spring and other cereals, rape, corn and clover being the primary crops. Most lapwings in this area breed in ploughed fields, spring cereals, meadows and winter wheat. Fishponds, the dominating type of wetlands, are used mainly for intensive carp production and every year some of them are drained in the spring and thus available to plovers for nesting.

Material and Methods

Field observations

The behaviour of lapwings was investigated during 113 h of observations at 63 nests on 13 breeding sites in the surroundings of Písek, České Budějovice basin, from late March till late May 1998–2002 and 2005. The nests were situated in colonies of various sizes and in different habitats (Table 1). Plovers were studied for a total of 54 h at 15 nests and 11 sites in the Třeboň basin, from late April till mid June in 2001–2003. Only solitary nests placed mostly on the bottoms of drained fishponds were found in this species. Moreover, three nests placed in a harvested peat bog, two nests in a sand pit and one nest in a flooded field adjacent to a river bed were included. The behaviour of incubating adults of both species and their responses to diurnal nest predators locating the nests by visual cues were monitored. Non-invasive direct observations from a car or from hides at field edges but at reliable distances from the territories were used without affecting the birds, using a combination of 20 x 60 binoculars and a 40 x 60 fixed telescope. In colonial lapwings (unlike in solitary breeding plovers), it was usually possible to observe more than one nest at a time. Continuous observations ran for 1– hours (mean 75 min. for lapwings and 60 min. for plovers).

Table 1. Distribution of studied nests of the lapwing *Vanellus vanellus* in colonies of various size (two to nine nests within a breeding group) and in different habitat types (spring crops, ploughed fields, meadows and winter wheat).

Colony size (no. nests within a group)	2	3	4	5	6	7	8	9	Total
no. nests studied	2	7	7	12	4	16	8	7	63
Habitat type	Spring crops		Ploughed f.		Meadows		Winter w.		Total
no. nests studied	21		8		24		10		63

We distinguished the following two main types of responses to an approaching predator: staying at the nest (continuing incubation) and leaving the nest (by flying or running away). If possible, we monitored also the behaviour following departure from the nest. This included either passive waiting in the territory, attacking the intruder or incubation-feigning. However, it was sometimes hard to make observations in lapwing colonies, because the birds were not individually marked. When flushed out by an approaching violator, all birds in a colony usually

mixed up, while some of them expelled the predator and some remained on the ground. Thus, only a limited set of observations is available for analysing behaviour after leaving the nest.

It was difficult to explicitly define the distance to which the reaction of incubating parents should be recorded. Territory size and shape are flexible due to variability of the habitat structure and the individuality of breeding birds in both species. Moreover, the nesting territories are often not contiguous and their borders are vague (C r a m p 1990). There are also differences in responses to various types of predators and their locomotion, such as walking or flying (W h i t t a m & L e o n a r d 2000). In general, warning calls and postures in both species may be recorded when the intruder appears 50–100 m away (E l l i o t 1985, C r a m p 1990, own observations). Thus, as a compromise, we defined this distance arbitrarily as a maximum of 100 m for both the lapwing and the plover. Potential predators appearing beyond this distance and those closer but concealed by vegetation (e.g. dense shrubs along fishpond edges) being out of view of incubating birds and thus undetected by them were not considered.

The possible sex effect on the reaction to predators (as shown in the lapwing by K i s e t al. 2000) was controlled for by maximising the total observation duration per nest and thus balancing the sample for both sexes (parents). The observations were made continuously, regardless of weather or time of the day (except reduced visibility during heavy rain, fog and dusk), between 06:30 a.m. and 06:30 p.m., as daily variation in the activity of predators on breeding grounds may influence the incubation patterns of the parents (S a s v a r i & H e g y i 2000). However, there was no reason to expect daily variation in individual responses to the same predator, so the time of the day was not considered as a predictor in the analyses.

The stage of incubation may affect the flushing distances in ducks according to predictions of the parental investment theory (A l b r e c h t & K l v a n a 2004). However, no effect of the incubation stage on frequency of attacks or on the time spent on attacks has been found in the lapwing (K i s e t al. 2000). There could be an important effect when comparing the incubation stage and the period of rearing the young (W h i t t a m & L e o n a r d 2000), but a significant shift in perception of the same predator species within the incubation stage itself is unlikely (W a l t e r s 1990). As we tried to spread the observations over the whole incubation period of the studied nests, we did not consider this factor in further analyses.

Statistical analysis

The responses of parents of both wader species to predators were fitted using generalized linear models with a logistic link function and binomial error term (GLM_{binom}). The effects of particular predator species (controlled for individual nests) were treated separately for the lapwing and plover data sets. To avoid pseudoreplications due to repeated observations at most nests (mean number of records = 7.4 per one nest in the lapwing and 4.3 in the plover), the records were summed for individual nests. These were analysed as independent units to examine the effects of colony size and habitat type in lapwings (no such data was available for plovers) and differences between behavioural responses of the two wader species toward the dominant predator, the carrion crow *Corvus corone*. Numbers of observations per nest were controlled for in these models. The χ^2 statistics or F-test (if the overdispersion of residual deviance was > 1 ; C r a w l e y 2002) were computed using the S-Plus software package (S-PLUS® 1999). We refer to significances based on Type III Sum of Squares.

Results

During observations of lapwings, nine species of nest predators were recorded within their breeding territories, with the black-headed gull *Larus ridibundus* being the most common (43% responses of lapwings). In plover breeding territories, the carrion crow was the commonest (50% responses of plovers) out of five predator species present (Table 2).

In total, we recorded 435 responses (either leaving the nest or staying at the nest and incubating the eggs) to the approaching nest predators in lapwings and 26 in plovers. Lapwings usually remained incubating and less frequently left the nests (29.6%), while plovers mostly left the nests (67.6%).

Table 2. Number of responses to nest predators observed in the breeding territories of lapwings *Vanellus vanellus* and plovers *Charadrius dubius*. Marsh harriers in plover territories were excluded from the analysis due to the potential predation risk for both nests and adults.

Species	lapwing <i>Vanellus vanellus</i>	plover <i>Charadrius dubius</i>
black-headed gull <i>Larus ridibundus</i>	187	4
marsh harrier <i>Circus aeruginosus</i>	102	-
carrion crow <i>Corvus corone</i>	79	15
black-billed magpie <i>Pica pica</i>	33	not observed
hen harrier <i>Circus cyaneus</i>	13	not observed
grey heron <i>Ardea cinerea</i>	10	4
European jay <i>Garrulus glandarius</i>	5	3
black stork <i>Ciconia nigra</i>	4	not observed
raven <i>Corvus corax</i>	2	not observed
Total	435	26

The responses of lapwings were not affected by colony size (GLM_{binom}: $F_{1,54} = 1.47$, $P = 0.23$) or habitat type ($F_{1,54} = 1.82$, $P = 0.17$) but varied significantly among predator species ($F_{7,369} = 1.47$, $P < 0.0001$; Fig. 1A), leaving the nest being a frequent but not prevailing behaviour in the presence of most predator species. Similar statistical significances (and thus not presented in this study) were obtained when we reduced the data set to the four most frequent predators, i.e. black-headed gull, marsh harrier (*Circus aeruginosus*), carrion crow and black-billed magpie (*Pica pica*).

The plovers responded differently to individual predator species ($\chi^2_{3,25} = 15.8$, $P = 0.0012$). However, they left the nests more frequently than lapwings; nest departures dominated as a response to an approaching violator in two of four predator species (Fig. 1B).

As the behaviour of lapwings and plovers was strongly dependent on the particular predator species, we reduced the comparison between the two waders to their responses to the carrion crow. This species has been found to be the most common nest predator at plover breeding grounds (from which our total data set is limited) and, moreover, it provoked most departures from nests in both waders (Fig. 1). This predator also caused significantly fewer departures from nests in lapwings (44.3%, $n = 34$ nests) than in plovers (87.5%, $n = 6$ nests; $F_{1,37} = 8.13$, $P = 0.007$).

Leaving the nest involved either flying or running away. In both species, this reaction was followed by attacks against intruders less frequently than by passive waiting, i.e. most of the breaks in incubation forced by predators were not followed by aggression towards predators (Table 3). Although departures from the nest followed by a predator attack appeared more commonly in lapwings (28.1%) than in plovers (13.3%), the differences between the two species were not

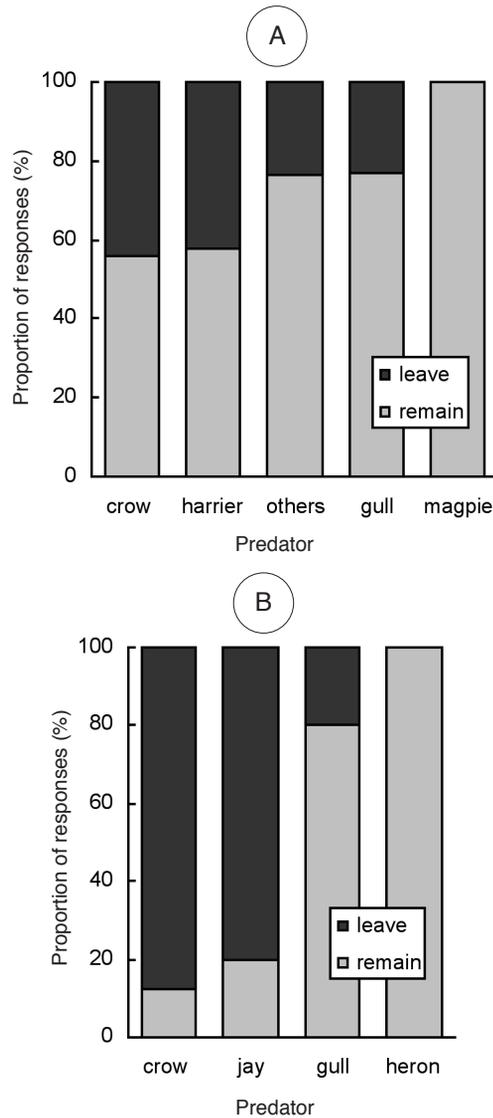


Fig. 1. Responses (leaving the nest or staying at the nest) of incubating lapwings *Vanellus vanellus* (A) and plovers *Charadrius dubius* (B) to approaching nest predators. The results are ordered according to the decreasing proportion of nest departures. The list of predators includes the following species: crow *Corvus corone*, harrier *Circus aeruginosus*, others (*Circus cyaneus*, *Ciconia nigra* and *Corvus corax*), gull *Larus ridibundus*, magpie *Pica pica*, jay *Garrulus glandarius* and heron *Ardea cinerea*.

significant ($F_{1,37} = 1.32$, $P = 0.26$). Instead of more frequent aggressive attacks, the plovers (but not lapwings) were repeatedly observed feigning incubation outside their real nest (Table 3).

Discussion

Our results suggest that both charadriids, the northern lapwing and the little ringed plover, may rely on egg crypsis as a reasonable antipredator strategy. Both species regularly left the

Table 3. Types of responses to approaching predators associated with departures from nests in lapwings *Vanellus vanellus* and plovers *Charadrius dubius*.

Species	Lapwing <i>Vanellus vanellus</i>		plover <i>Charadrius dubius</i>	
Responses to carrion crows				
	N	%	N	%
Flying away	13 (9 nests)	38.2	-	-
Running away	11 (10 nests)	32.4	10 (6 nests)	71.4
Incubation-feigning	-	-	4 (2 nests)	28.6
Predator attack	10 (8 nests)	29.4	-	-
Total	34 (16 nests)	100	14 (6 nests)	100
Responses to all nest predators except carrion crows				
	N	%	N	%
Flying away	51 (16 nests)	54.3	1 (1 nest)	11.1
Running away	17 (6 nests)	18.1	2 (1 nest)	22.2
Incubation-feigning	-	-	4 (2 nests)	44.5
Predator attack	26 (10 nests)	27.6	2 (1 nest)	22.2
Total	94 (17 nests)	100	9 (2 nests)	100

nest without subsequently attacking the approaching common nest predators, such as corvids (carrion crow, European jay) or black-headed gulls. However, lapwings departed from the nests less frequently than plovers, suggesting that the two species differ in the extent to which this behavioural trait is used. Unlike plovers, breeding lapwings prefer an alternative strategy associated with colonial nesting and larger body size, both of them providing efficient harassment and exclusion of predators from nesting territories (Elliott 1985, Larsen et al. 1996). In addition, lapwings can incubate more tightly while their partners guarding the nests are ready to attack the intruders (Sasvari & Hegyi 2000). As shown previously by Cresswell (1997), species that actively defend their nests are assumed to show little correlation between the risk of nest predation and nest concealment. Nevertheless, the importance of masking the nest location by lapwing parents is well demonstrated when the birds return to the nest. They usually alight not right at the nest but a few tens of meters away from it. As soon as they land, they walk or run directly or round to the nest (Crampton 1990, own observations).

The reduced amount of lapwing departures from the nests in the presence of nest predators may become advantageous particularly when predator densities are high. The northern lapwing starts to breed early in the season and incubating birds often experience cold weather, which substantially raises their energy requirements (Lislevand 2001). Thus, too frequent departures from the nest might have a detrimental effect on egg hatchability and on overall breeding success. Indeed, the colonial antipredator strategy of northern lapwings seems to ensure favourable hatching success also in areas with high incidence of predators (Sasvari & Hegyi 2000).

In contrast, small and cryptic plovers frequently responded to the approaching predators, particularly corvids, by leaving the nest. We suppose that when the incubating plovers detect a nest predator in time, they tend to hide the nest location more thoroughly than lapwings, due to their limited ability to defend the nest actively. When staying at the nest, the parent may disclose the clutch by showing its location to the predator (Sutch 1949, Cresswell 1997, Roper & Goldstein 1997, Muchai & du Plessis 2005). Our hypothesis can be indirectly supported by an additional behavioural trait shown

by the plover – luring the predator away by false incubation outside the nest (Cramp 1990, this study). Also unlike lapwings, plovers regularly use another behavioural element, injury-feigning, which may switch the attention of a predator to the adult, while the plover draws away from the nest (Cramp 1990). However, this behaviour is more typically during the brood-rearing than during the egg-incubation period (own unpubl. observations). In our study, only one lapwing male was observed exerting short elements of injury-feigning and distraction while attacking a small group of roe deer (*Capreolus capreolus*) in the proximity of the clutch (own unpubl. observation).

We did not find any effects of colony size or habitat (in lapwings) on behavioural responses to predators. In contrast, decision making of adults in both species varied strongly according to the predator species approaching the territory (see also Cramp 1990). Most departures from the nests occurred in the presence of corvids, which are considered highly skilled generalist predators of bird clutches in farmlands (Elliot 1985, Luginbuhl et al. 2001, Roos 2002, Olsen 2003, Šálek 2004).

We conclude that both wader species may commonly use passive reliance on egg crypsis as a possible way of protecting their nests against visually oriented predators. However, both of them also combine it with active behavioural elements such as predator attacks and/or incubation-feigning. Departure from the nest seems to be unprofitable as an exclusive form of nest protection, because attractive prey (eggs) primarily evolves to be cryptic, and crypsis itself may activate the search image attention processes (Speed 2000), at least in some imaginative predators such as corvids searching ingeniously for easy and nutritious food.

Acknowledgements

We thank Tomáš Albrecht for constructive comments on the manuscript and Jaroslav Cepák for assistance in the field. We are thankful to Robin Haley for his help with improving our presentation in English. This study was supported by the Czech Science Foundation (GAČR grant no. 206/97/P092).

LITERATURE

- Albrecht T. & Klvaňa P. 2004: Nest crypsis, reproductive value of a clutch and escape decisions in incubating female mallards *Anas platyrhynchos*. *Ethology* 110: 603–613.
- Blanco G. & Bertellotti M. 2002: Differential predation by mammals and birds: implications for egg-colour polymorphism in a nomadic breeding seabird. *Biol. J. Linn. Soc.* 75: 137–146.
- Cramp S. (ed.) 1990: Handbook of the Birds of Europe, the Middle East and North Africa: The Birds of the Western Palearctic. Vol. 3: Waders to gulls. *Oxford Univ. Press, Oxford*.
- Crawley M. J. 2002: Statistical Computing. An Introduction to Data Analysis using S-Plus. *John Wiley & Sons Ltd., Chichester*.
- Cresswell W. 1997: Nest predation: the relative effects of nest characteristics, clutch size and parental behaviour. *Anim. Behav.* 53: 93–103.
- Elliot R. D. 1985: The exclusion of avian predators from aggregations of nesting lapwings (*Vanellus vanellus*). *Anim. Behav.* 33: 308–314.
- Fitzpatrick S. & Bouchez B. 1998: Effects of recreational disturbance on the foraging behaviour of waders on a rocky beach. *Bird Study* 45: 157–171.
- Glutz von Blotzheim U. N., Bauer K. M. & Bezzel E. 1975: Handbuch der Vögel Mitteleuropas. Bd. 6. *Akademische Verlagsgesellschaft, Wiesbaden*.
- Haskell D. G. 1996: Do bright colors at nests incur a cost due to predation? *Evolutionary Ecology* 10: 285–288.
- Hegyí Z. & Sasvári L. 1998: Parental condition and breeding effort in waders. *J. Anim. Ecol.* 67: 41–53.
- Hockey P. A. R. 1982: Adaptiveness of nest-site selection and egg coloration in the African Black Oystercatcher *Haematopus moquini*. *Behav. Ecol. Sociobiol.* 11: 117–123.

- Hudec K. & Štátný K. (eds) 2005: Fauna ČR, Ptáci – Aves. Díl II/1. Sv. 29/1. *Academia, Praha*.
- Jimenez J. E. & Conover M. R. 2001: Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. *Wildl. Soc. Bull.* 29: 62–69.
- Kis J., Liker A. & Székely T. 2000: Nest defence by Lapwings: observations on natural behaviour and an experiment. *Ardea* 88: 155–163.
- Koivula K. & Rönkä A. 1998: Habitat deterioration and efficiency of antipredator strategy in a meadow-breeding wader, Temminck's stint (*Calidris temminckii*). *Oecologia* 116: 348–355.
- Larsen T. & Grungetjern S. 1997: Optimal choice of neighbour: predator protection among tundra birds. *J. Avian Biol.* 28: 303–308.
- Larsen T., Sordahl T. A. & Byrkjedal I. 1996: Factors related to aggressive nest protection behaviour: a comparative study of Holarctic waders. *Biol. J. Linn. Soc.* 58: 409–439.
- Lauro B. & Nol E. 1995: Patterns of habitat use for Pied and Sooty Oystercatchers nesting at the Furneaux Islands, Australia. *Condor* 97: 920–934.
- Lislevand T. 2001: Male incubation in Northern Lapwings: effects on egg temperature and potential benefits to females. *Ornis Fennica* 78: 23–29.
- Lloyd P., Plagányi É., Lepage D., Little R. M. & Crowe T. M. 2000: Nest-site selection, egg pigmentation and clutch predation in the ground-nesting Namaqua Sandgrouse *Pterocles namaqua*. *Ibis* 142: 123–131.
- Luginbuhl J. M., Marzluff J. M., Bradley J. E., Raphael M. G. & Varland D. E. 2001: Corvid survey techniques and the relationship between corvid relative abundance and nest predation. *J. Field Ornithol.* 72: 556–572.
- Martin T. E. 1993: Nest predation among vegetation layers and habitat types – revising the dogmas. *Am. Nat.* 141: 897–913.
- Moreno J. & Osorno J. L. 2003: Avian egg colour and sexual selection: does eggshell pigmentation reflect female condition and genetic quality? *Ecology Letters* 6: 803–806.
- Muchai M. & du Plessis M. A. 2005: Nest predation of grassland bird species increases with parental activity at the nests. *J. Avian Biol.* 36: 110–116.
- Olsen H. 2003: Patterns of predation on ground nesting meadow birds. *Ph.D. thesis, The Royal Veterinary and Agricultural University, Copenhagen*.
- Roos S. 2002: Functional response, seasonal decline and landscape differences in nest predation risk. *Oecologia* 133: 608–615.
- Roper J. J. & Goldstein R. R. 1997: A test of the Skutch hypothesis: does activity at nests increase nest predation risk? *J. Avian Biol.* 28: 111–116.
- Sanchez J. M., Corbacho C., Del Viejo A. M. & Parejo D. 2004: Colony-site tenacity and egg color crypsis in the gull-billed tern. *Waterbirds* 27: 21–30.
- Sasvari L. & Hegyi Z. 2000: Avian predators influence the daily time budget of lapwings *Vanellus vanellus*. *Folia Zool.* 49: 211–219.
- Schekkerman H., van Roomen M. W. J. & Underhill L. G. 1998: Growth, behaviour of broods and weather-related variation in breeding productivity of Curlew Sandpipers *Calidris ferruginea*. *Ardea* 86: 153–168.
- Skutch A. F. 1949: Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430–455.
- Solis J. C. & Delope F. 1995: Nest and egg crypsis in the ground-nesting stone curlew *Burhinus oedicephalus*. *J. Avian Biol.* 26: 135–138.
- Speed M. P. 2000: Warning signals, receiver psychology and predator memory. *Anim. Behav.* 60: 269–278.
- S-PLUS® 1999: S-PLUS for Windows 2000. Guide to Statistics. *Data Analysis Products Division, MathSoft, Seattle, 1999*.
- Šálek M. 2004: The spatial pattern of the black-billed magpie, *Pica pica*, contribution to predation risk on dummy nests. *Folia Zool.* 53: 57–64.
- Thyen S. & Exo K. M. 2005: Interactive effects of time and vegetation on reproduction of redshank (*Tringa totanus*) breeding in Wadden Sea salt marshes. *J. Orn.* 146: 215–225.
- Walters J. R. 1990: Anti-predatory behavior of lapwings: field evidence of discriminative abilities. *Wilson Bull.* 102: 49–70.
- Westmoreland D. & Kiltie R. A. 1996: Egg crypsis and clutch survival in three species of blackbirds (Icteridae). *Biol. J. Linn. Soc.* 58: 159–172.
- Whittam R. M. & Leonard M. L. 2000: Characteristics of predators and offspring influence nest defense by Arctic and Common Terns. *Condor* 102: 301–306.
- Whittingham M. J., Percival S. M. & Brown A. F. 2002: Nest-site selection by golden plover: why do shorebirds avoid nesting on slopes? *J. Avian Biol.* 33: 184–190.
- Yanes M. & Suarez F. 1995: Nest predation patterns in ground-nesting passerines on the Iberian peninsula. *Ecography* 18: 423–428