

Nest cameras do not affect nest survival in a meadow-nesting shorebird

VOLKER SALEWSKI*  and LUIS SCHMIDT

Michael-Otto-Institut im NABU, Goosstroot 1, 24861 Bergenhusen, Germany.

*Author for correspondence; email: Volker.Salewski@NABU.de

(Received 1 September 2020; revision accepted 18 November 2020)

Summary

Identifying the fate of birds' nests and the causes of breeding failure is often crucial for the development of conservation strategies for threatened species. However, collecting these data by repeatedly visiting nests might itself contribute to nest failure or bias. To solve this dilemma, automatic cameras have increasingly been used as a time-efficient means for nest monitoring. Here, we consider whether the use of cameras itself may influence hatching success of nests of the Black-tailed Godwit *Limosa limosa* at two long-term study sites in northern Germany. Annually between 2013 and 2019, cameras were used to monitor godwit nests. In 2014 and 2019, nests were randomly equipped with cameras or not, and nest survival checked independently of the cameras. Nest-survival models indicated that survival probabilities varied between years, sites and with time of the season, but were unaffected by the presence of cameras. Even though predation is the main cause of hatching failure in our study system, we conclude that predators did not learn to associate cameras with food either when the cameras were initially installed or after they had been used for several years. Cameras were thus an effective and non-deleterious tool to collect data for conservation in this case. As other bird species may react differently to cameras at their nests, and as other sets of predators may differ in their ability to associate cameras with food, the effect of cameras on breeding success should be carefully monitored when they are used in a new study system.

Keywords: Black-tailed Godwit, hatching success, *Limosa limosa*, nest predation, camera

Introduction

Reproductive success is one of the key demographic parameters influencing the dynamics of bird populations. Its determination and the analyses of ultimate and proximate causes of reproductive failure are critical for the conception of conservation strategies and the validation of management measures for many threatened species (Green 1999, Robinson *et al.* 2014, Brown and Graham 2015). Often, however, a dilemma arises in pursuit of these goals: in order to investigate reproduction, researchers need to approach reproducing birds and their nest sites, and this disturbance might itself cause nest failure. Frequent visits to nests are needed to investigate clutch survival probabilities, number of hatchlings, cause of reproductive failure etc., and usually the knowledge gained is positively correlated with the number of visits to active nests (Mayfield 1975, Verboven *et al.* 2001, Andes *et al.* 2019). However, more frequent visits may increase the probability of reproductive failure, especially when the time interval between visits is short (Lenington 1979, Salathe 1987,

Major 1990, Bêty and Gauthier 2001, Teunissen *et al.* 2006). Nests may be more prone to predation when unattended because of disturbance by researchers (MacInnes and Misra 1972, Westmoreland and Best 1985, Major 1990), repeatedly flushing birds of from nests may direct the attention of predators to nests (Lenington 1979), predators could learn to follow human scent to nests (Snelling 1968, Whelan *et al.* 1994), or predators may even directly follow investigators to nests (Strang 1980).

Automatically triggered cameras (hereafter 'cameras') may offer an efficient solution to this dilemma because they allow permanent monitoring without repeated disturbance. Cameras have been used to monitor bird nests since the 1950s (Gysel and Davis 1956, Royama 1959, Cox *et al.* 2012). Since the early 1970s, the number of publications reporting use of cameras has constantly increased (Cox *et al.* 2012). In recent decades, technical improvement, miniaturization and decreasing costs have further promoted the use of cameras in ornithological research (Cox *et al.* 2012). The introduction of new technology in research often raises the question of whether and how the technology itself affects the result of the study (Ibáñez-Alamo *et al.* 2012). With respect to cameras monitoring bird nests the crucial question is whether the installation or presence of a camera influences reproductive success. For example, the installation of cameras could either lead to decreasing reproductive success if predators learn to associate cameras with prey (attraction effect), or they could lead to an increase in reproductive success if predators tend to avoid unfamiliar structures or human scent in their environment (deterrence effect) (Buler and Hamilton 2000, Herranz *et al.* 2002, Richardson *et al.* 2009, Herring *et al.* 2011, Ellis-Felege and Carroll 2012, Weston *et al.* 2017) or predators could simply ignore cameras. However, in many studies using cameras, the devices' influence on results has not been assessed.

Since 2013, we have used cameras to monitor hatching success and causes of hatching failure of nests of the Black-tailed Godwit *Limosa limosa*. The Black-tailed Godwit nests on the ground in meadows and open grasslands in the Palaearctic, and young are precocial. The central European subspecies *L. l. limosa* has declined dramatically over most of its range during recent decades (Gill *et al.* 2007, Kentie *et al.* 2016). Habitat transformation due to changing land use practices has been the main threat to populations in central Europe (Schekkerman *et al.* 2008, Kleijn *et al.* 2010). The immediate demographic cause of the decrease is low reproductive success due to high clutch and chick mortality, both of which have increased in recent decades (Roodbergen *et al.* 2012). Predation pressure on clutches and chicks has apparently increased in recent decades too (Bellebaum 2002, Roodbergen *et al.* 2012, Kentie *et al.* 2013), and is now the main cause of nest failure and chick mortality at many sites. This often leads to reproductive rates insufficient to maintain stable populations and knowing the cause of breeding failure is, therefore, the key for successful management (Valkama and Currie 1999, MacDonald and Bolton 2008, Schekkerman *et al.* 2009, Roodbergen *et al.* 2012).

At the beginning of our project, we showed that the application of cameras did not reduce the survival prospects of clutches of Black-tailed Godwits (Salewski and Schmidt 2016). However, potential predators may need some time to learn to associate cameras with a valuable food resource, i.e. to develop a 'search image' (Tinbergen 1960, Langley 1996, Dukas and Kamil 2001). Thus, even though the application of cameras may not reduce hatching success immediately, it may do so in the future (Lenington 1979) though the validity of the concept of a 'search image' is controversial (e.g. Krebs 1973, Guilford and Dawkins 1987, Reid and Shettleworth 1992). To determine if there is a lag effect on nest success due to learned behaviour by predators, we repeated our experiment after five years of continuous application of cameras. Here, we present an analysis of the effect of cameras on daily nest survival probabilities, which suggests that there is no such effect even after continuous use.

Methods

Study sites

Field work was conducted in two North Sea coast polders in Schleswig-Holstein, northern Germany: Beltringharder Koog (BeK; 54.561°N, 8.903°E) and Dithmarscher Speicherkoog Süd

(SpS; 54.047°N, 9.002°E). Data for this study were collected in 2014 and 2019 as described below. In 2013 and 2015 to 2018, in the framework of a broader study on hatching success and nest predation of Black-tailed Godwit, similar routines were followed and almost all nests were equipped with cameras, thus allowing for potential long-term effects of cameras to occur.

Field work

From early April to mid-June, we searched for nests of Black-tailed Godwits. At a distance of c. 3 m, nests were marked with one bamboo stick with a small flag. The hatching date was estimated using the 'floating method' (van Paassen *et al.* 1984). Unless otherwise designated (see below), a camera (Moultrie Game Spy M-990i or M-999i) was mounted on a wooden post at a distance of 1.5–3.0 m from the nests and at a height of 30–80 cm (Figure 1). All nests (i.e. with or without a camera) were subsequently visited and checked at intervals of 2–5 days to document their fate. Broken eggs in or near a nest or the disappearance of the eggs before the presumed hatching date were indications of failure. Chicks or the presence of many small eggshell fragments in the nest indicated hatching success (Green *et al.* 1987).

Nests inside an anti-predator fence, or in parcels with livestock, have not been included in our analysis. Vertical structures such as cameras attract cattle and, therefore, increase the risk of trampling (Beintema and Müskens 1987). We left every third Black-tailed Godwit nest without a camera in 2014 and every second in 2019, thus creating a random distribution of nests with and without a camera. However, some additional nests were excluded from the analysis as they were abandoned, or their fate remained unclear. One nest that was included in a preliminary analysis (Salewski and Schmidt 2016) from BeK was not considered here because it could not be ruled out that it had already been abandoned before we found it.

Statistical analysis

We used nest survival models implemented in the programme MARK to estimate the daily survival probability ϕ of Black-tailed Godwit clutches (Dinsmore *et al.* 2002), using only visit data. The analyses started with the generation of encounter histories for each nest, which included information about the day when the nest was found, the last day the nest was alive, the last day the nest was checked, and the fate of the nest. In order to avoid positive bias in the estimates of ϕ by potentially considering exposure days after nests hatched, for successful nests we excluded days after the last check at which the nest was active (Dinsmore *et al.* 2002).

Beside the presence of a camera, other factors could cause variation in godwit nest success. Previous studies have shown that hatching probability can vary between sites (Nehls 2001, Schekkerman *et al.* 2006, Salewski *et al.* 2016), between years (Groen and Hemerik 2002, Teunissen *et al.* 2008), and with time within the breeding season (Schroeder *et al.* 2006, Kentie *et al.* 2015). Therefore, we included a camera effect (nest either with or without camera), a site effect (nest in SpS or BeK), a year effect (nest found in 2014 or in 2019), and a time effect t (ϕ varies daily throughout the breeding season) in our global model ($[\phi(\text{camera}*\text{site}*\text{year}*t)]$, Table 1). Competing models were all combinations of these factors, including all possible interactions, models that considered only one of these factors, and a model that assumed that ϕ does not vary with any of these factors [$\phi(.)$]. We have previously shown that ϕ showed a constant trend (T) throughout the breeding season (Salewski *et al.* 2016). Therefore, we only considered t in the global model, but T in all other models including a time effect. This left us with a set of 17 models (Table 1). Competing models were ranked according to their AIC_C values (Burnham and Anderson 2002). We considered a $\Delta\text{AIC}_C > 2$ between the most parsimonious model and any competing model as indicating that the competing model has considerably less support (Burnham and Anderson 2002).



Figure 1. Black-tailed Godwit clutch with camera.

Results

Our analysis used data from 141 nests, which included 32 nests from BeK in 2014 (20 with camera of which 11 hatched and eight were depredated and one was abandoned, 12 without camera of which seven hatched and five were depredated), 34 nests from SpS in 2014 (19 with camera of

Table 1. Models to estimate daily survival probability (ϕ) of Black-tailed Godwit clutches at two sites in northern Germany. 'T' denotes a constant trend throughout the breeding season and 't' a variation with each day of the breeding season. 'site' and 'year' denote variations between sites and years, respectively.

Model	AIC _C	Δ AIC _C	AIC _C weight	N Parameter
$\phi(T^*site^*year)$	414.340	0	0.658	8
$\phi(T^*year)$	416.610	2.271	0.211	4
$\phi(site^*year)$	418.587	4.247	0.079	4
$\phi(T^*camera^*year)$	421.304	6.964	0.031	8
$\phi(.)$	423.445	9.105	0.011	1
$\phi(T)$	423.810	9.470	0.009	2
$\phi(year)$	424.261	9.922	0.005	2
$\phi(camera)$	424.396	10.056	0.004	2
$\phi(site)$	425.142	10.802	0.003	2
$\phi(camera^*site^*year)$	425.578	11.239	0.002	8
$\phi(T^*camera)$	426.629	12.290	0.001	4
$\phi(camera^*year)$	426.955	12.615	0.001	4
$\phi(T^*camera^*site^*year)$	427.170	12.830	0.001	16
$\phi(T^*site)$	427.569	13.229	0.001	4
$\phi(camera^*site)$	428.059	13.720	0.001	4
$\phi(T^*camera^*site)$	434.215	19.875	<0.001	8
$\phi(camera^*site^*year^*t)$	2175.140	1760.800	<0.001	568

which seven hatched and 12 were depredated, 15 without camera of which four hatched and 11 were depredated), 37 nests from BeK in 2019 (18 with camera of which eight hatched and 10 were depredated, 19 without camera of which 14 hatched and four were depredated and one was abandoned), and 38 nests from SpS in 2019 (19 with camera of which 12 hatched and seven were depredated, 19 without camera of which 10 hatched and nine were depredated).

The most parsimonious model was the model including the factors T (constant trend over time), site and year, as well as their interactions ($[\phi(T^*site^*year)]$, Table 1). There was little support for any model that included 'camera'.

AIC_C weights are probabilities that can be summed across models containing factors of interest to represent the relative weight of support for that factor. The sums of the AIC_C weights across all models containing 'year', 'T' and 'site' were 0.988, 0.912 and 0.745, respectively, whereas the sum of AIC_C weights for the factor 'camera' was only 0.041.

Discussion

Our analysis of data from Black-tailed Godwit nests with or without a camera provides the conclusion that daily survival probabilities vary between sites and years, and over time within the breeding season, but not with the installation of cameras. This is in line with a number of previous studies on ground-nesting meadow, sea- and shorebirds that found no change in predation probabilities when nests were equipped with cameras. Examples are White-rumped Sandpiper *Calidris fuscicollis* and Baird's Sandpiper *C. bairdii* in Canada (McKinnon and Bêty 2009), Banded Dotterel *Charadrius bicinctus* and Black-fronted Tern *Sterna albostriata* in New Zealand (Sanders and Maloney 2002), St. Helena Plover *Charadrius sanctaehelenae* on St. Helena in the South Atlantic Ocean (Burns *et al.* 2013), and Northern Lapwing *Vanellus vanellus* on the British Isles (Bolton *et al.* 2007). A study on Northern Lapwing and Black-tailed Godwit clutches in The Netherlands provided similar results: daily survival probability was lower in nests with video-cameras than nests without cameras in one out of six study sites, in one site survival probabilities were higher in nests with a video-camera, and in the other four sites survival probabilities did not differ (Teunissen *et al.* 2008). A meta-analysis also failed to find a general effect of the installation of cameras at bird nests on their survival (Richardson *et al.* 2009). Additionally, other markers such

as sticks at nests of Black-tailed Godwits and Northern Lapwing did not increase predation (Beintema and Müskens 1987, Zámečník *et al.* 2018; see also Hannon *et al.* 1993). In contrast, a higher predation rate of clutches equipped with cameras compared to clutches without cameras was found in the White-rumped Sandpiper *Calidris fuscicollis* (Cantar and Montgomerie 1985). However, the replacement of cameras three times during 2.5 days, but probably no similar frequency of close visits at the control group, was a massive disturbance that could have biased nest failure (McKinnon and Bêty 2009). Thus, in the literature there is a broad consensus that the appropriate use of nest cameras does not affect hatching success of ground nesting birds (see also Sanders and Maloney 2002, Herring *et al.* 2011, Mallord *et al.* 2012, Ellis-Felege and Carroll 2012, Andes *et al.* 2019).

We also showed that there was no effect of cameras on survival probabilities of clutches even after these had been applied for several years. Hence, there is no indication that predators learn to associate cameras with valuable and predictable resources even when they had the chance to become familiar with them over an extended period of time. Nocturnal predators, that rely on visual as well as on olfactory cues to find food (Conover 2007), are responsible for the majority of clutch failures of Black-tailed Godwits in our study area with three species, red fox *Vulpes vulpes*, raccoon dog *Nyctereutes procyonoides* and polecat *Mustela putorius*, responsible for 89% of all attributable predations. Diurnal birds that rely exclusively on visual cues to find food (e.g. Engel *et al.* 2020), accounted for only 5.1% (corvids 1.7%, raptors 3.4%) of attributable losses (Salewski *et al.* 2019), although they were permanently present throughout the breeding season (unpubl. data). There are indications that birds, especially corvids, may learn to associate human activities and markers at or near bird and reptile nests with food (Yahner and Wright 1985, Götmark 1992, Miller and Hobbs 2000, Rollinson and Brooks 2007), although this could not be confirmed by Andes *et al.* (2019) with respect to cameras. Nevertheless, a different set of prevailing predators, for example corvids, and predators that may react on cameras in different ways (Meek *et al.* 2016) may lead to different results. Further, other bird species may differ in their reaction to cameras at their nests (Thompson *et al.* 1999, Pietz and Granfors 2000) compared to Black-tailed Godwits, which readily accept cameras (pers. obs.). Therefore, cameras should be applied with caution in new projects, especially when they have never been used in the target species before. Their effect on the parameters studied should be carefully explored to avoid spurious results and, as a consequence, mislead conservation strategies.

Cameras are an effective tool for monitoring the fate of Black-tailed Godwit clutches and identifying the cause of failure (Salewski and Schmidt 2019, Salewski *et al.* 2019). In contrast, the information gathered by other methods is limited. Thermologgers are only able to detect the time when incubation stops (e.g. Teunissen *et al.* 2008). Inference from cues such as egg remains (Green *et al.* 1987, Bellebaum and Boschert 2003) can cause misidentification of predators or misinterpretation of the fate of clutches (Larivière 1999, Liebezeit and George 2003, Coates *et al.* 2008, Staller *et al.* 2005, Macdonald and Bolton 2008, Ellis-Felege and Carroll 2012, Andes *et al.* 2019, Salewski *et al.* 2019). The use of cameras is thus the only reliable method to identify nest predators to species level and to obtain other insights into the breeding ecology of birds through continuous monitoring with minimal disturbance (Cox *et al.* 2012, Andes *et al.* 2019). Cameras are an indispensable tool for basic research on breeding ecology and, therefore, provide basic information for the development of an evidence-based management of threatened species.

Acknowledgements

We are grateful to D. V. Cimiotti, A. Evers, H. Hötter and B. Klinner-Hötter for their help in the field. We thank the Landesamt für Landwirtschaft, Umwelt und ländliche Räume des Landes Schleswig-Holstein and the Bundeswehr especially the team of the WTD71, for the support in the BEK and SPS respectively. D. Franklin kindly improved our English. This is a publication of the EU LIFE Project LIFE-Limosa (LIFE11 NAT/DE/000353 LIFE-Limosa).

References

- Andes, A. K., Shaffer, T. L., Sherfy, M. H., Hofer, C. M., Dovichin, C. M. and Ellis-Felege, S. N. (2019) Accuracy of nest fate classification and predator identification from evidence at nests of Least Terns and Piping Plovers. *Ibis* 161: 286–300.
- Beintema, A. J., Müskens, G. J. D. M. (1987) Nesting success of birds breeding in Dutch agricultural grasslands. *J. Appl. Ecol.* 24: 743–758.
- Bellebaum, J. (2002) Prädation als Gefährdung bodenbrütender Vögel in Deutschland – eine Übersicht. *Ber. Vogelschutz* 39: 95–117.
- Bellebaum, J. and Boschert, M. (2003) Bestimmung von Predatoren an Nestern von Wiesenvögeln. *Vogelwelt* 124: 83–91.
- Béty, J. and Gauthier, G. (2001) Effects of nest visits on predator activity and predation rate in a Greater Snow Goose colony. *J. Field Ornithol.* 72: 573–586.
- Bolton, M., Butcher, N., Sharpe, F., Stevens, D. and Fisher, G. (2007) Remote monitoring of nests using digital camera technology. *J. Field Ornithol.* 78: 213–220.
- Brown, L. M. and Graham, C. H. (2015) Demography, traits and vulnerability to urbanization: can we make generalizations? *J. Appl. Ecol.* 52: 1455–1464.
- Burnham, K. P. and Anderson, D. R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. New York, USA: Springer.
- Buler, J. J. and Hamilton, R. B. (2000) Predation of natural and artificial nests in a southern pine forest. *Auk* 117: 739–747.
- Burns, F., McCulloch, N., Székely, T. and Bolton, M. (2013) The impact of introduced predators on an island endemic, the St Helena Plover, *Charadrius sanctaehelena*. *Bird Conserv. Internatn.* 23: 125–135.
- Cantar, R. V. and Montgomerie, R. D. (1985) The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. *Behaviour* 95: 261–289.
- Coates, P. S., Connelly, J. W. and Delehanty, D. J. (2008) Predators of Greater Sagegrouse nests identified by video monitoring. *J. Field Ornithol.* 79: 421–428.
- Conover, M. R. (2007) *Predator-prey dynamics. The role of olfaction*. Boca Raton, USA: CRC Press.
- Cox, W. A., Pruett, M. S., Benson, T. J., Chiavacci, S. J. and Thompson, F. R. (2012) Development of camera technology for monitoring nests. Pp. 185–210 in C. A. Ribic, F. R. Thompson and P. J. Pietz, eds. *Video surveillance of nesting birds*. Studies in Avian Biol. 43.
- Dinsmore, S. J., White, G. C. and Knopf, F. L. (2002) Advanced techniques for modeling avian nest survival. *Ecology* 83: 3476–3488.
- Dukas, R. and Kamil, A. C. (2001) Limited attention: the constraint underlying search image. *Behav. Ecol.* 12: 192–199.
- Ellis-Felege, S. N. and Carroll, J. P. (2012) Gamebirds and nest cameras: present and future. Pp. 35–44 in C. A. Ribic, F. R. Thompson and P. J. Pietz, eds. *Video surveillance of nesting birds*. Studies in Avian Biol. 43.
- Engel, N., Végváry, Z., Rice, R., Kubelka, V. and Székely, T. (2020) Incubating parents serve as visual cues to predators in Kentish plover (*Charadrius alexandrinus*). *PLoS ONE* 15: e0236489.
- Gill, J. A., Langston, R. H. W., Alves, J. A., Atkinson, P. W., Bogher, P., Vieira, N. C., Crockford, N. J., Gélineau, G., Groen, N., Gunnarsson, T. G., Hayhow, B., Hooijmeijer, J., Kentie, R., Kleijn, D., Lourenço, P. M., Masero, J. A., Meunier, F., Potts, P. M., Roodbergen, M., Schekkerman, H., Schröder, J., Wymenga, E. and Piersma, T. (2007) Contrasting trends in two Black-tailed Godwit populations: a review of causes and recommendations. *Wader Study Group Bull.* 114: 43–50.
- Götmark, F. (1992) The effect of investigator disturbance on nesting birds. *Curr. Ornithol.* 9: 63–104.
- Green, R. E. (1999) Applications of large-scale studies of demographic rates to bird conservation. *Bird Study* 46 (Supplement): S279–S288.
- Green, R. E., Hawell, J. and Johnson, T. H. (1987) Identification of predators of wader eggs from egg remnants. *Bird Study* 34: 87–91.
- Groen, N. M. and Hemerik, L. (2002) Reproductive success and survival of Black-tailed

- Godwits *Limosa limosa* in a declining local population in the Netherlands. *Ardea* 90: 239–248.
- Guilford, T. C. and Dawkins, M. S. (1987) Search images not proven: a reappraisal of recent evidence. *Anim. Behav.* 35: 1838–1845.
- Gysel, L. W. and Davis, E. M. (1956) A simple automatic photographic unit for wildlife research. *J. Wildl. Manage.* 20: 451–453.
- Hannon, S. J., Martin, K., Thomas, L. and Schieck, J. (1993) Investigator disturbance and clutch predation in Willow Ptarmigan: methods for evaluating impact. *J. Field Ornithol.* 64: 575–586.
- Herranz, J., Yanes, M. and Suárez, F. (2002) Does photo-monitoring affect nest predation? *J. Field Ornithol.* 73: 97–101.
- Herring, G., Ackerman, J. T., Takekawa, J. Y., Eagles-Smith, C. A. and Eadie, J. M. (2011) Identifying nest predators of American Avocets (*Recurvirostra americana*) and Black-Necked Stilts (*Himantopus mexicanus*) in San Francisco Bay, California. *Southw. Naturalist* 56: 35–43.
- Ibáñez-Álamo, J. D., Sanllorente, O. and Soler, M. (2012) The impact of researcher disturbance on nest predation rates: a meta-analysis. *Ibis* 154: 5–14.
- Kentie, R., Booth, C., Hooijmeijer, J. C. E. W. and Piersma, T. (2015) Management of modern agricultural landscapes increases nest predation rates in Black-tailed Godwits *Limosa limosa*. *Ibis* 157: 614–625.
- Kentie, R., Hooijmeijer, J. C. E. W., Trimbos, K. B., Groen, N. M. and Piersma, T. (2013) Intensified agricultural use of grasslands reduces growth and survival of precocial shorebird chicks. *J. Appl. Ecol.* 50: 243–251.
- Kentie, R., Senner, N. R., Hooijmeijer, J. C. E. W., Márquez-Ferrando, R., Figuerola, J., Masero, J. A., Verhoeven, M. A. and Piersma, T. (2016) Estimating the size of the Dutch breeding population of Continental Black-tailed Godwits from 2007–2015 using resighting data from spring staging sites. *Ardea* 114: 213–225.
- Kleijn, D., Schekkerman, H., Dimmers, W. J., van Kats, R. J. M., Melman, D. and Teunissen, W. A. (2010) Adverse effects of agricultural intensification and climate change on breeding habitat quality of Black-tailed Godwits *Limosa l. limosa* in the Netherlands. *Ibis* 152: 475–486.
- Krebs J. R. (1973) Behavioral aspects of predation. Pp. 72–111 in P. P. G. Bateson and P. H. Klopfer, eds. *Perspectives in ethology*. Boston, USA: Springer.
- Langley, C. M. (1996) Search images: Selective attention to specific visual features of prey. *J. Experimental Psychol.: Anim. Behav. Processes* 22: 152–163.
- Larivière, S. (1999) Reasons why predators cannot be inferred from nest remains. *Condor* 101: 718–721.
- Lenington, S. (1979) Predators and Blackbirds: The "uncertainty principle" in field biology. *Auk* 96: 190–192.
- Liebezeit, J. R. and George, T. L. (2003) Comparison of mechanically egg-triggered cameras and time-lapse video cameras in identifying predators at Dusky Flycatcher nests. *J. Field Ornithol.* 74: 261–269.
- MacDonald, M. A. and Bolton, M. (2008) Predation on wader nests in Europe. *Ibis* 150 (Suppl. 1): 54–73.
- MacInnes, C. D. and Misra, R. K. (1972) Predation on Canada Goose nests at McConnell River, Northwest Territories. *J. Wildl. Manage.* 36: 414–422.
- Major, R. E. (1990) The effect of human observers on the intensity of nest predation. *Ibis* 132: 608–612.
- Mallord, J. W., Orsman, C. J., Cristinacce, A., Butcher, N., Stowe, T. J. and Charman, E. C. (2012) Mortality of Wood Warbler *Phylloscopus sibilatrix* nests in Welsh oakwoods: predation rates and the identification of nest predators using miniature nest cameras. *Bird Study* 59: 286–295.
- Mayfield, H. F. (1975) Suggestions for calculating nest success. *Wilson Bull.* 87: 456–466.
- McKinnon, L. and Bêty, J. (2009) Effect of camera monitoring on survival rates of High Arctic shorebird nests. *J. Field Ornithol.* 80: 280–288.
- Meek, P., Ballard, G., Fleming, P. and Falzon, G. (2016) Are we getting the full picture? Animal responses to camera traps and implications for predator studies. *Ecol. Evol.* 6: 3216–3225.
- Miller, J. R. and Hobbs, N. T. (2000) Recreational trails, human activity, and nest

- predation in lowland riparian areas. *Landscape Urban Planning* 50: 227–236.
- Nehls, G. (2001) Entwicklung der Wiesenvogelbestände im Naturschutzgebiet Alte-Sorge-Schleife, Schleswig-Holstein. *Corax* 18 (Sonderheft 2): 81–101.
- Pietz, P. J. and Granfors, D. A. (2000) Identifying predators and fates of grassland passerine nests using miniature video cameras. *J. Wildl. Manage.* 64: 71–87.
- Reid, P. J. and Shettleworth, S. J. (1992) Detection of cryptic prey: Search image or search rate? *J. Experimental Psychol.: Anim. Behav. Processes* 18: 273–286.
- Richardson, T. W., Gardali, T. and Jenkins, S. H. (2009) Review and meta-analysis of camera effects on avian nest success. *J. Wildl. Manage.* 73: 287–293.
- Robinson, R. A., Morrison, C. A. and Baillie, S. R. (2014) Integrating demographic data: towards a framework for monitoring wildlife populations at large spatial scales. *Methods Ecol. Evol.* 5: 1361–1372.
- Rollinson, N. and Brooks, R. J. (2007) Marking nests increases the frequency of nest depredation in a northern population of Painted Turtles (*Chrysemys picta*). *J. Herpetol.* 41: 174–176.
- Roodbergen, M., van der Werf, B. and Hötker, H. (2012) Revealing the contribution of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. *J. Ornithol.* 153: 53–74.
- Royama, T. (1959) A device of an auto-cinematic food-recorder. *Japanese J. Ornithol.* 15: 172–176.
- Salathe, T. (1987) Crow predation on Coot eggs: effects of investigator disturbance, nest cover and predator learning. *Ardea* 75: 221–229.
- Salewski, V. and Schmidt, L. (2016) Beeinflussen Nestkameras den Schlupferfolg von Uferschnepfen *Limosa limosa*. *Ber. Vogelwarte Hiddensee* 23: 47–57.
- Salewski, V. and Schmidt, L. (2019) The raccoon dog - an important new nest predator of black-tailed Godwit in northern Germany. *Wader Study* 126: 28–34.
- Salewski, V., Schmidt, L., Evers, A., Klinner-Hötker, B. and Hötker, H. (2016) Bruterfolg von Uferschnepfen *Limosa limosa* in Schleswig-Holstein. *Vogelkd. Ber. Niedersachs.* 44: 245–258.
- Salewski, V., Evers, A. and Schmidt, L. (2019) Wildkameras ermitteln Verlustursachen von Gelegen der Uferschnepfe (*Limosa limosa*). *Natur und Landschaft* 94: 59–65.
- Sanders, M. D. and Maloney, R. F. (2002) Causes of mortality at nests of ground-nesting birds in the Upper Waitaki Basin, South Island, New Zealand: a 5-year video study. *Biol. Conserv.* 106: 225–236.
- Schekkerman, H., Teunissen, W. and Oosterveld, E. (2006) Breeding success of Black-tailed Godwits *Limosa limosa* under 'mosaic management', an experimental agri-environment scheme in The Netherlands. *Osnabrücker Naturwiss. Mitt.* 32: 131–136.
- Schekkerman, H., Teunissen, W. and Oosterveld, E. (2008) The effect of 'mosaic management' on the demography of black-tailed godwit *Limosa limosa* on farmland. *J. Appl. Ecol.* 45: 1067–1075.
- Schekkerman, H., Teunissen, W. and Oosterveld, E. (2009) Mortality of Black-tailed Godwit *Limosa limosa* and Northern Lapwing *Vanellus vanellus* chicks in wet grasslands: influence of predation and agriculture. *J. Ornithol.* 150: 133–145.
- Schroeder, J., Hooijmeijer, J., Both, C. and Piersma, T. (2006) The importance of early breeding in Black-tailed Godwits (*Limosa limosa*). *Osnabrücker Naturwiss. Mitt.* 32: 239–241.
- Snelling, J. C. (1968) Overlap in feeding habits of Red-winged Blackbirds and Common Grackles nesting in a Cattail marsh. *Auk* 85: 560–585.
- Staller, E. L., Palmer, W. E., Carroll, J. P., Thornton, R. P. and Sisson, D. C. (2005) Identifying predators at Northern Bobwhite nests. *J. Wildl. Manage.* 69: 124–132.
- Strang, C. A. (1980) Incidence of avian predators near people searching for waterfowl nests. *J. Wildl. Manage.* 44: 220–222.
- Teunissen, W., Schekkerman, H. and Willems, F. (2006) Predation on meadowbirds in The Netherlands – results of a four year study. *Osnabrücker Naturwiss. Mitt.* 32: 137–143.
- Teunissen, W., Schekkerman, H., Willems, F. and Majoor, F. (2008) Identifying predators of eggs and chicks of Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*) in the Netherlands and the importance of predation on wader reproductive output. *Ibis* 150: 74–85.

- Thompson, F. R., Dijak, W. and Burhans, D. E. (1999) Video identification of predators at songbird nests in old fields. *Auk* 116: 259–264.
- Tinbergen, L. (1960) The natural control of insects in pine woods I. Factors influencing the intensity of predation by songbirds. *Archives Néerlandaises de Zoologie* 13: 265–343.
- Valkama, J. and Currie, D. (1999) Low productivity of Curlews *Numenius arquata* on farmland in southern Finland: Causes and consequences. *Ornis Fennica* 76: 65–70.
- van Paassen, A. G., Veldman, D. H. and Beintema, A. J. (1984) A simple device for determination of incubation stages in eggs. *Wildfowl* 35: 173–178.
- Verboven, N., Ens, B. J. and Dechesne, S. (2001) Effect of investigator disturbance on nest attendance and egg predation in Eurasian Oystercatchers. *Auk* 118: 503–508.
- Westmoreland, D. and Best, L. B. (1985) The effect of disturbance on Mourning Dove nesting success. *Auk* 102: 774–780.
- Weston, M. A., Ekanayake, K. B., Lomas, S., Glover, H. K., Mead, R. E., Cribbin, A., Tan, L. X. L., Whisson, D. A., Maguire, G. S. and Cardilini, A. P. A. (2017) Case studies of motion-sensing cameras to study clutch survival and fate of real and artificial ground-nests in Australia. *Bird Study* 64: 476–491.
- Whelan, C. J., Dilger, M. L., Robson, D., Hallyn, L., Dilger, S. (1994) Effects of olfactory cues on artificial-nest experiments. *Auk* 111: 945–952.
- Yahner, R. H. and Wright A. L. (1985) Depredation on artificial ground nests: Effects of edge and plot age. *J. Wildl. Manage.* 49: 508–513.
- Zámecník, V., Kubelka, V. and Sálek, M. (2018) Visible marking of wader nests to avoid damage by farmers does not increase nest predation. *Bird Conserv. Internatn.* 28: 293–301.