# NEST DESERTION: AN ANTI-PREDATOR STRATEGY OF THE AUSTRALIAN FAIRY TERN *STERNULA NEREIS NEREIS*

CLAIRE N. GREENWELL[1*,2], JAMES N. DUNLOP[1,3] & NEIL R. LONERAGAN[1,2]

[1]*Environmental and Conservation Sciences, Murdoch University, 90 South Street, Murdoch, Western Australia 6150, Australia*
**(C.Greenwell@murdoch.edu.au)*
[2]*Centre for Sustainable Aquatic Ecosystems, Harry Butler Institute, Murdoch University, 90 South Street, Murdoch, Western Australia 6150, Australia*
[3]*Conservation Council of Western Australia, Lotteries West House, 2 Delhi Street, West Perth, Western Australia 6150, Australia*

*Received 20 February 2019, accepted 01 May 2019*

**ABSTRACT**

GREENWELL, C.N., DUNLOP, J.N. & LONERAGAN, N.R. 2019. Nest desertion: An anti-predator strategy of the Australian Fairy Tern *Sternula nereis nereis*. *Marine Ornithology* 47: 193–197.

This study describes nest desertion as a probable but previously undescribed anti-predator strategy for the Australian Fairy Tern *Sternula nereis nereis*. Deserted nests were observed at night for up to nine nights following the laying of the first eggs at a colony in southwestern Australia. Nocturnal nest desertion may provide the terns with a mechanism for assessing the occurrence of potential nest predators, maintaining reproductive synchrony, and reducing the total time a colony is detectable by predators. Additionally, temporary diurnal nest desertion for up to 80 minutes was observed following the predation of an adult tern. Diurnal nest desertion may be used to reduce the risk of adult mortality and, consequently, decrease colony visibility, thereby increasing reproductive success.

**Key words:** Egg neglect, Laridae, predation, reproductive success, *Sternula*

## INTRODUCTION

Predation is one of the most influential selection pressures on animal reproductive strategies because it shapes the heritable behavioural and reproductive traits of a species (Lack 1968, Lima & Dill 1990, Martin 1992, Šmejkal *et al.* 2018). Birds have evolved various strategies that reduce predation during the breeding season to enhance adult survival and lifetime productivity and to increase the survival of offspring (Lack 1968, Martin 1992, Ward *et al.* 2011).

Surface-nesting seabirds, including members of the Laridae family, usually breed in groups or colonies, and active anti-predator behaviours such as nest synchronisation and social mobbing play an important role in reducing predation on the colony (Lack 1968, Gochfeld 1980). However, nest predation remains an important source of breeding failure. Colonies provide an opportunity to reward predators over an extended time because of the high density of nests, eggs, and adult birds, which may attract greater numbers of predators and repeat visits by predators over time (Gochfeld 1980, Burger & Gochfeld 1991, Martin 1992, Danchin & Wagner 1997, Ward *et al.* 2011). Where adults are not threatened directly (i.e., only eggs and chicks are targeted), the presence of a predator usually elicits aggressive aerial defence to drive off the intruder (Burger & Gochfeld 1991). However, where predators pose an immediate threat to adult survival, broods are routinely left unattended until the threat subsides; in extreme cases, a nesting attempt may be abandoned altogether (Burger & Gochfeld 1991, Levermann & Tøttrup 2007, CNG unpubl. data). For example, systematic predation of endangered Black-fronted Terns *Chlidonias albostriatus* (probably by cats) in New Zealand resulted in the deaths of six adults (10 % of the population) and the subsequent abandonment of all 28 nests in the colony (O'Donnell *et al*. 2010).

In Greenland, the presence of a persistent arctic fox *Alopex lagopus* at a mixed colony of Arctic Terns *Sterna paradisaea* (311 pairs) and Sabine's Gulls *Xema sabini* (67 pairs) during a year of late sea ice break-up resulted in nesting attempts being delayed until the colony was eventually completely abandoned (Levermann & Tøttrup 2007). Prey availability was ruled out as a contributing factor, as courting birds were observed returning to the colony with a steady supply of large fish (Levermann & Tøttrup 2007).

Other anti-predator adaptations among surface-nesting seabirds include synchrony of egg-laying, crypsis of eggs and chicks, and nesting at densities that reduce the risk of predation to any one individual breeding adult (Lack 1968, Gochfeld 1980, Oro 1996, Brunton 1999). The eggs and chicks of surface-nesting seabirds have a mottled appearance and are very inconspicuous, and this crypsis is enhanced by parents routinely incorporating shells, small stones, and organic material in and around the nest (Lack 1968, Burger & Gochfeld 1991, Parrish & Pulham 1995). When faced with the threat of predation, chicks often lay flat against the substratum and rely on their cryptic colouration to reduce the probability of detection (Lack 1968, Burger & Gochfeld 1991).

Delayed nocturnal occupation of colony sites (prior to egg-laying) and nest desertion (after egg-laying) are two anti-predator strategies that are less studied, but they have been documented for several larids, including Least Tern *Sternula antillarum* (delayed nocturnal occupation; Atwood & Massey 1988, Wilson *et al.* 1991), Sandwich Tern *Thalasseus sandvicensis* (delayed nocturnal occupation; Veen 1977), and Common Tern *Sterna hirundo* (nocturnal nest desertion; Marshall 1942, Nisbet 1975, Shealer & Kress 1991). Roosting away from colony sites before the peak egg-laying period and/or deserting nests at night during the egg-laying and hatching periods

probably decrease predation by reducing both adult mortality and the length of time that the colony is detectable to nocturnal predators (Nisbet 1975, Atwood 1986). Predation of adult Common Terns by Great Horned Owls *Bubo virginianus* at a colony in Massachusetts is believed to have been the proximate cause of nocturnal nest desertion; this resulted in the delayed hatching of eggs by about six days and increased predation of unattended chicks (Nisbet 1975).

Our study describes nocturnal and diurnal nest desertion behaviour of the Australian Fairy Tern *Sternula nereis nereis* during the early egg-laying and the post-laying periods. To our knowledge, this behaviour has not been reported previously for the Fairy Tern.

## MATERIALS AND METHODS

### Study species

The Fairy Tern is one of two small terns, along with the Little Tern *Sternula albifrons*, to nest in Australia. In 2011, the Fairy Tern was listed as Vulnerable, in accordance with s266B of the Environment Protection and Biodiversity Conservation Act 1999 (Cwlth), due to a substantial population contraction (24 % between 1974 and 2007) and to a lack of evidence demonstrating that threats affecting Fairy Terns were abating (DE 2011, TSSC 2011). In the approved Conservation Advice for Fairy Terns, major threatening processes included introduced predators (e.g., red foxes *Vulpes vulpes*, cats *Felis catus*, and black rats *Rattus rattus*) and increased natural predators, whose populations are exacerbated due to human impacts (e.g., Silver Gulls *Chroicocephalus novaehollandiae*, Australian Ravens *Corvus coronoides*) (DE 2011).

### Study area

We focused on two sites that are managed for Fairy Tern conservation in southwestern Australia, both located within 100 km of the Perth metropolitan centre (Fig. 1). The first site was situated in Mandurah (32°31′14.24″S, 115°43′00.26″E) and managed by the City of Mandurah (Fig. 1). It covers an area of ~2 460 $m^2$, has a uniform elevation of ~2.0 m above sea level, and is separated from the adjoining beach by a 1.5-m limestone sea wall. The second site is located on reclaimed land at Rous Head, North Fremantle (32°02′25.83″S, 115°44′23.69″E) and is managed by the Fremantle Ports (Fig. 1). It covers a total area of ~3 250 $m^2$ of which ~1 650 $m^2$ is suitable for nesting, has an elevation of ~5.0 m above sea level, and is surrounded by coastal vegetation. The perimeters of both sites are fully enclosed by a chain-wire fence that is 1.2 m high and lined with shade-cloth to provide protection to nesting terns and their young. A layer of shell material was added to the ground surface at both sites by land managers in previous years to increase substrate complexity, thus enhancing the attractiveness of the sites to breeding terns and increasing crypsis to predators.

Observations of nocturnal nest desertion were made at Mandurah 19–24 October 2018 prior to sunrise and 20–30 October after last light. Nest desertion was observed at North Fremantle on 10–11 November and on an ad hoc basis from 29 November to 06 December 2018, either after last light or before sunrise. Observations of diurnal nest desertion were documented at North Fremantle between 05 December and 07 January 2019 during regular visits to the site in the morning (~04h30–09h00) and afternoon (~16h00–19h30). The monitoring at North Fremantle was less extensive and more opportunistic than at Mandurah in the early nesting period due to logistical constraints. Three wildlife cameras (Swift 3C, Queensland) were installed on 22 October 2018 to monitor colony development at the North Fremantle site.

All observations were conducted in accordance with Murdoch University Animal Ethics Committee Approval (Protocol 546, Permit RW3077/18).

## RESULTS

### Nocturnal nest desertion (Mandurah)

Night desertion of nests was first observed at Mandurah on 19 October 2018, with terns not returning to the colony site until the following morning. The first three nests were recorded on 19 October (Nest 1 = N1), 22 October (Nest 2 = N2), and 23 October (Nest 3 = N3), and eggs were not incubated continuously during the day. The colony site was abandoned in the late afternoon, usually between 17h00 and 18h30, and the terns did not return to resume incubation until after sunrise the following morning. Fairy Terns were not observed after dark at the nest site until 29 October, so the eggs appear to have been left unattended for up to nine consecutive nights (N1). Fairy Terns were observed roosting on the adjacent beach at first light on 22 October and on the evening of 25 October. On 24 October, Fairy Terns were heard in the distance but were not seen on the beach.

The egg from N1 had hatched by 21 November (~33 d after it was laid), and the observed chick was estimated to be ~1–2 d old. Eggs from N2 were damaged during a hail storm and did not hatch. It is unclear whether the eggs from N3 were incubated and hatched.

### Nocturnal nest desertion (North Fremantle)

Evidence of nocturnal nest desertion was also recorded in the early egg-laying period (29 November to 03 December 2018) at North Fremantle. On 29 November, three Fairy Terns were present following last light, but no terns were present prior to sunrise on 01 December, despite two nests being evident. Three birds were incubating eggs on 02 December at first light (6 nests recorded), as were two birds on 03 December (11 nests recorded).

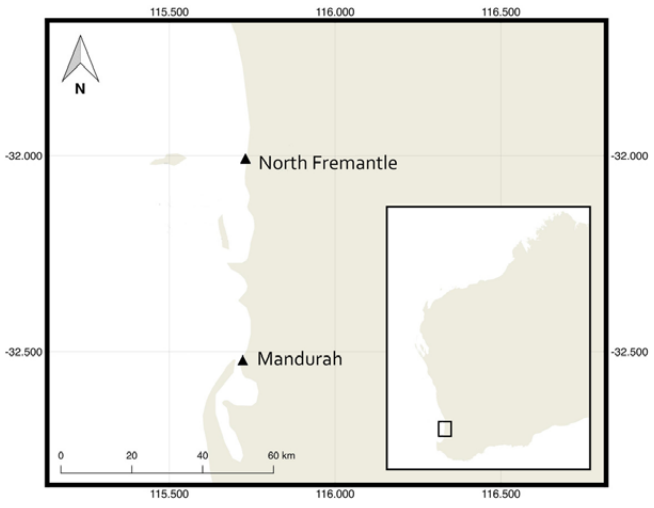


**Fig. 1.** Map showing the locations of two managed sanctuary sites for the Australian Fairy Tern in the Perth metropolitan area, southwestern Australia.

**Diurnal nest desertion (Rous Head)**

On 17 December 2018 at 06h05 an Australian Hobby *Falco longipennis* swooped into the Rous Head colony and captured a nesting adult Fairy Tern. This event resulted in the up-flight of the entire colony and temporary abandonment of the site. Highly synchronised group flight behaviour, similar to that exhibited by small shorebirds and described by Atwood (1986) for Least Terns at night roost locations, was observed for several minutes until the birds were so far away that they could no longer be observed from the colony site. At 06h56 the terns returned to within close proximity of the colony site and their flight behaviour remained highly synchronised, although several small groups broke away before re-joining the main group. Several group passes were made over the colony site between 07h03 and 07h14. Some birds landed momentarily before the group swooped synchronously down over the sea wall and out over the water, before circling back over the colony site. Unlike regular noisy up-flights that occur with no apparent stimuli, the flock remained almost completely silent while in flight. By 07h25 most birds had settled back onto the site, before up-flighting again, en masse, with no apparent stimulus between 07h31 and 07h33.

An attempted predation event by a hobby was also observed on the previous day (16 December) at 07h08. The falcon swooped into the colony, this time failing to capture a tern. This attempt resulted in all but one of the nesting Fairy Terns up-flighting and deserting the colony site, after which the falcon departed the area. Synchronised group flight behaviour was observed, but on this occasion, the birds remained within sight of the colony and the flight was initially silent, becoming noisier over time. The birds remained in flight for ~27 min, with most individuals landing at 07h35. Despite these events, the colony was successful, with a maximum of ~220 active nests established; it produced an estimated mean of 0.74 fledglings per pair (CNG & JND unpubl. data).

## DISCUSSION

This study describes temporary nest desertion by Fairy Terns at the beginning of egg-laying, a strategy probably used to reduce adult predation, shorten the period of adult exposure to predators, and assess egg and chick predators during the breeding season. To our knowledge, this behaviour has not previously been described for Fairy Terns.

**Nocturnal nest desertion**

Nocturnal colony desertion and egg abandonment was observed for up to nine consecutive nights (19–29 October 2018) at Mandurah. Despite this abandonment, the first egg laid was viable, hatching ~31 d after the initial laying date. This egg was incubated continuously for ~22 d following the initial nine nights of no incubation. Note that the average incubation period for Fairy Tern eggs is 21 d ($n$ = 82; CNG unpubl. data). Therefore, the temporary abandonment of eggs at night probably delayed hatching for the length of time that the egg was not continuously incubated (i.e., ~9 d). Nest desertion was also observed in the North Fremantle colony, although it is difficult to quantify the extent of this behaviour because this site could not be monitored to the same degree as Mandurah. These observations highlight the potential for eggs to remain viable in the early egg-laying period despite long periods (≥ 14 h) without incubation and to remain undetected by potential egg predators, such as Nankeen Night Heron *Nycticorax caledonicus*.

Plasticity in incubation is not widely described among coastal foraging seabirds, but notable examples of egg neglect do occur, particularly among pelagic-foraging birds such as auklets, murrelets, and storm petrels (Sealy 1976, Boersma 1979, Murray *et al.* 1980, Blight *et al.* 2010). Such behaviour in pelagic seabirds is believed to be an adaptation to patchily distributed food resources; this enables adults to spend more time foraging, especially in the early post–egg laying period, without compromising egg viability (Boersma 1979, Blight *et al.* 2010). For example, eggs of the Fork-tailed Storm Petrel *Oceanodroma furcata* were commonly neglected for up to two days at a time (mean cumulative egg-neglect period = 11 d), but in some instances, viable eggs were deserted for periods of 4–7 d (Boersma 1979). For coastal seabirds, whose food resources are typically more abundant and easier to access than pelagic seabirds, nocturnal nest desertion or egg neglect may be a strategy to pre-emptively avoid predation (Nisbet 1975, Nuechterlein & Buitron 2002).

Nocturnal nest desertion by Fairy Terns in the early egg-laying period is probably a mechanism to reduce predation in three ways: (1) it provides a mechanism for assessing potential nest predators, (2) it enhances reproductive synchrony in the early egg-laying period, and (3) it reduces the total time the colony is detectable to potential predators (Nisbet 1975, Gochfeld 1980, Atwood 1986, Jovani & Grimm 2008). Note that we recorded no instances of egg predation during the nocturnal desertion period, despite the site being accessible to mammalian egg-predators. However, predation by cats or black rats may have occurred for previous nesting attempts in Mandurah, and cats are suspected of predating chicks and adults later in the 2018/19 season. A cat was detected at North Fremantle on 22 October, long before any eggs were laid, and it was removed by animal control agents. Baiting for black rats in the sea wall adjoining the sanctuary during the colony's formation period at both sites may have helped to relieve pressure from this well-known egg predator.

Habitat selection by nesting birds represents a compromise between maximising resources and minimising losses to adverse environmental conditions and predation. The first birds to lay eggs at any given location take the greatest risk, as the individual risk of predation is higher than for birds nesting mid-season (Ashmole 1963, Nisbet 1975). Nocturnal nest desertion was first described in Common Terns by Marshall (1942) in Ohio and subsequently by Nisbet (1975) in Massachusetts. While an explanation for nocturnal nest desertion was not apparent in Ohio, predation by Great Horned Owls is thought to have been the proximate cause of temporary desertion in Massachusetts (Marshall 1942, Nisbet 1975).

The lack of egg predation following nocturnal desertion may provide the terns with information about an absence of nest predators. Night observations of the North Fremantle colony prior to egg-laying revealed night-prospecting (i.e., flying over the site without landing) by Fairy Terns for short periods of time, but terns did not land on the site. Night-prospecting may also be used to provide terns with information on site suitability and the presence of potential predators. On an evolutionary timescale, predation by alien species is a relatively recent threat to breeding seabirds (Weidinger 1998). However, small terns frequently shift colony sites from one breeding attempt to the next (Nisbet 1973, Burger 1984, Cabot & Nisbet 2013). This regular shifting of colony sites in response to predation, by either native or introduced species, demonstrates a well-developed mechanism for rapid reaction through learning (Burger 1984, Weidinger 1998) among the small terns.

Nocturnal desertion of eggs increases the time to hatching (Nisbet 1975), but such behaviour may also be used to enhance reproductive synchrony. The adaptive value of synchronous hatching is thought to increase survival through: (1) collective group defence; (2) predator swamping, whereby high prey-population densities reduce individual risk by overwhelming the predator population's ability to consume them; and (3) predator confusion, which reduces the efficiency of prey capture (Lack 1968, Hamilton 1971, Estes 1976, Ims 1990). As Nisbet (1975) points out, predators have the potential to take a larger proportion of prey when fewer individuals are present. Thus, nesting in the middle of the season may increase the chance of survival for an individual when a larger proportion of birds are nesting (Nisbet 1975).

Observations of nocturnal nest desertion at multiple colony sites in the absence of nocturnal predators suggests that this is an innate, adaptive behavioural strategy used to enhance reproductive success, rather than a direct behavioural response to nocturnal adult predation (Nisbet 1975).

**Diurnal nest desertion (North Fremantle)**

Diurnal nest desertion and flocking by Fairy Terns is, presumably, a strategy used to increase adult survival, despite the potential cost to eggs and chicks (Thompson *et al.* 1974, Caraco *et al.* 1980, Burger & Gochfeld 1991). Seabirds are long-lived, with high adult survivorship (Hunt 1980)—for example, the current longevity record for the Australian Fairy Tern is ~22 years (banded in 1997 by JND; Australian Bird and Bat Banding Scheme pers. comm.). Therefore, the potential to replace themselves can be achieved by numerous nesting attempts over their long lifespan (Furness & Monaghan 1987, Schreiber & Burger 2001, Bried & Jouventin 2002). Thus, a reduction in short-term reproductive investment far outweighs any risk to future survival associated with a single mating attempt (Boersma 1979, Bried & Jouventin 2002, Drent & Daan 2002).

The flocking behaviour of birds is widely thought to decrease the chance of predation, with larger flocks having a higher probability of detecting potential predators and a lower risk of individual predation (Siegfried & Underhill 1975, Caraco *et al.* 1980). In the Common Starling *Sturnus vulgaris*, flocks became increasingly compact and synchronised with increased predation pressure, and predation rates by Peregrine Falcon *Falco peregrinus* were greatest at roosts where flocking behaviour was less marked (Carere *et al.* 2009). Therefore, the highly synchronised group flight behaviour and deliberate offshore movement by Fairy Terns is likely undertaken to reduce adult predation (Carere *et al.* 2009).

Secondly, nest desertion likely reduces nest detection by potential predators, which increases the chances of reproductive success, particularly for early- and mid-season nesters (Coulson 1966, Atwood 1986). Each breeding attempt is energetically costly, and birds breeding earlier in the season (closer to peak food availability) are typically more successful than those that lay later or birds laying for the second time (Coulson 1966). Therefore, reducing colony detectability, as opposed to completely abandoning the colony site, may be a strategy used to enhance reproductive success (Safina & Burger 1983). This behaviour overcomes the need to invest time and energy in the re-laying of eggs at an alternative site, which may yield low reproductive success (Safina & Burger 1983).

**ACKNOWLEDGEMENTS**

Special thanks to Cherilyn Corker and Rebecca Cassells for their very generous assistance in monitoring the Mandurah colony site after dark. Thanks also to the many volunteers that offered their time to assist with the Mandurah Fairy Tern Project and to the City of Mandurah for their support. Financial support was provided by Murdoch University, Fremantle Ports, Stuart Leslie Bird Award & BirdLife Australia, and Holsworth Wildlife Research Endowment & Ecological Society of Australia. Peter Dann offered comments that helped to improve our paper.

**REFERENCES**

ASHMOLE, N.P. 1963. The biology of the Wideawake or Sooty Tern *Sterna fuscata* on Ascension Island. *Ibis* 103b: 297–351.

ATWOOD, J.L. 1986. Delayed nocturnal occupation of breeding colonies by Least Terns (*Sterna antillarum*). *The Auk* 103: 242–244.

ATWOOD, J.L. & MASSEY, B.W. 1988. Site fidelity of Least Terns in California. *The Condor* 90: 389–394. doi:10.2307/1368567

BLIGHT, L.K., BERTRAM, D.F., WILLIAMS, T.D. & COWEN, L. 2010. Interannual variation in egg neglect and incubation routine of Rhinoceros Auklets *Cerorhinca monocerata* during the 1998–1999 El Niño/La Niña events. *Marine Ornithology* 38: 11–15.

BOERSMA, P.D. 1979. Egg neglect in the Procellariiformes: Reproductive adaptations in the Fork-tailed Storm-petrel. *The Condor* 81: 157–165. doi:10.2307/1367282

BRIED, J. & JOUVENTIN, P. 2002. Site and mate choice in seabirds: An evolutionary approach. In: SCHREIBER, E.A. & BURGER, J. (Eds.) *Biology of Marine Birds.* Boca Raton, USA: CRC Press.

BRUNTON, D. 1999. "Optimal" colony size for Least Terns: An inter-colony study of opposing selective pressures by predators. *The Condor* 101: 607–615. doi:10.2307/1370190

BURGER, J. 1984. Colony stability in Least Terns. *The Condor* 86: 61–67. doi:10.2307/1367347

BURGER, J. & GOCHFELD, M. 1991. *The Common Tern: Its Breeding Biology and Social Behavior*. New York, USA: Columbia University Press.

CABOT, D. & NISBET, I. 2013. *Terns.* Collins New Naturalist Library, Book 123. London, UK: Harper Collins.

CARACO, T., MARTINDALE, S. & PULLIAM, H.R. 1980. Avian flocking in the presence of a predator. *Nature* 285: 400–401. doi:10.1038/285400a0

CARERE, C., MONTANINO, S., MORESCHINI, F. ET AL. 2009. Aerial flocking patterns of wintering starlings, *Sturnus vulgaris*, under different predation risk. *Animal Behaviour* 77: 101–107. doi:10.1016/J.ANBEHAV.2008.08.034

COULSON, J.C. 1966. The influence of the pair-bond and age on the breeding biology of the Kittiwake Gull *Rissa tridactyla*. *Journal of Animal Ecology* 35: 269–279. doi:10.2307/2394

DANCHIN, E. & WAGNER, R.H. 1997. The evolution of coloniality: The emergence of new perspectives. *Trends in Ecology and Evolution* 12: 342–347. doi:10.1016/S0169-5347(97)01124-5

DEPARTMENT OF THE ENVIRONMENT (DE) 2011. *Approved conservation advice for* Sternula nereis nereis *(Fairy Tern).* Canberra: Department of the Environment and Energy, Australian Government. [Available online at http://www.environment.gov.au/biodiversity/threatened/species/pubs/82950-conservation-advice.pdf, accessed 24 October 2018.]

DRENT, R.H. & DAAN, S. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea* 55: 225–252. doi:10.5253/arde.v68.p225

ESTES, R.D. 1976. The significance of breeding synchrony in the wildebeest. *African Journal of Ecology* 14: 135–152. doi:10.1111/j.1365-2028.1976.tb00158.x

FURNESS, R.W. & MONAGHAN, P. 1987. *Seabird Ecology.* New York, USA: Chapman and Hall.

GOCHFELD, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. In: BURGER, J., OLLA, B.L., WINN, H.E. (Eds.) *Behavior of Marine Animals.* Boston, USA: Springer-Verlag US. doi:10.1007/978-1-4684-2988-6_7

HAMILTON, W.D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31: 295–311. doi:10.1016/0022-5193(71)90189-5

HUNT, G.L. 1980. Mate selection and mating systems in seabirds. In: BURGER, J., OLLA, B.L., WINN, H.E. (Eds.) *Behavior of Marine Animals.* Boston, USA: Springer-Verlag US. doi:10.1007/978-1-4684-2988-6_4

IMS, R.A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. *The American Naturalist* 136: 485–498. doi:10.1086/285109

JOVANI, R. & GRIMM, V. 2008. Breeding synchrony in colonial birds: From local stress to global harmony. *Proceedings of the Royal Society B: Biological Sciences* 275: 1557–1563. doi:10.1098/rspb.2008.0125

LACK, D. 1968. *Ecological adaptations for breeding in birds*. London, UK: Methuen.

LEVERMANN, N. & TØTTRUP, A.P. 2007. Predator effect and behavioral patterns in Arctic Terns (*Sterna paradisaea*) and Sabine's Gulls (*Xema sabini*) during a failed breeding year. *Waterbirds* 30: 417–420.

LIMA, S.L. & DILL, L.M. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology* 68: 619–640. doi:10.1139/z90-092

MARSHALL, N. 1942. Night desertion by nesting Common Terns. *The Wilson Bulletin* 54: 25–31.

MARTIN, T.E. 1992. Interaction of nest predation and food limitation in reproductive strategies. In: POWER, D.M. (Ed.) *Current Ornithology, Volume 9.* Boston, USA: Springer-Verlag US. doi:10.1007/978-1-4757-9921-7_5

MURRAY, K.G., WINNETT-MURRAY, K. & HUNT, G.L., JR. 1980. Egg neglect in Xantus' Murrelet. *Proceedings of the Colonial Waterbird Group* 3: 186–195.

NISBET, I.C.T. 1973. Terns in Massachusetts: Present numbers and historical changes. *Bird-Banding* 44: 27–55. doi: 10.2307/4511926

NISBET, I.C.T. 1975. Selective effects of predation in a tern colony. *The Condor* 77: 221–226. doi:10.2307/1365803

NUECHTERLEIN, G.L. & BUITRON, D. 2002. Nocturnal egg neglect and prolonged incubation in the Red-necked Grebe. *Waterbirds* 25: 485–491. doi:10.1675/1524-4695(2002)025[0485:NENAPI]2.0.CO;2

O'DONNELL, C.F.J., SEDGELEY, J.A. & VAN HAL, J. 2010. Variation in house cat (*Felis catus*) predation sign at a Black-fronted Tern (*Sterna albostriata*) colony. *Notornis* 57: 43–47.

ORO, D. 1996. Colonial seabird nesting in dense and small sub-colonies: An advantage against aerial predation. *The Condor* 98: 848–850. doi:10.2307/1369868

PARRISH, G.R. & PULHAM, G.A. 1995. Observations on the breeding of the New Zealand Fairy Tern. *Tane* 35: 161–173.

SAFINA, C. & BURGER, J. 1983. Effects of human disturbance on reproductive success in the Black Skimmer. *The Condor* 85: 164–171. doi:10.2307/1367250

SCHREIBER, E.A. & BURGER, J. 2001. Seabirds in the marine environment. In: SCHREIBER, E.A. & BURGER, J. (Eds.) *Biology of Marine Birds.* Boca Raton, USA: CRC Press.

SEALY, S.G. 1976. Biology of nesting Ancient Murrelets. *The Condor* 78: 294–306. doi:10.2307/1367688

SHEALER, D.A. & KRESS, S.W. 1991. Nocturnal abandonment response to Black-crowned Night-Heron disturbance in a Common Tern colony. *Colonial Waterbirds* 14: 51–56. doi:10.2307/1521279

SIEGFRIED, W.R. & UNDERHILL, L.G. 1975. Flocking as an anti-predator strategy in doves. *Animal Behaviour* 23: 504–508. doi:10.1016/0003-3472(75)90126-8

ŠMEJKAL, M., SOUZA, A.T., BLABOLIL, P. ET AL. 2018. Nocturnal spawning as a way to avoid egg exposure to diurnal predators. *Scientific Reports* 8: 15377. doi:10.1038/s41598-018-33615-4

THOMPSON, W.A., VERTINSKY, I. & KREBS, J.R. 1974. The survival value of flocking in birds: A simulation model. *Journal of Animal Ecology* 43: 785–820. doi:10.2307/3537

THREATENED SPECIES SCIENTIFIC COMMITTEE (TSSC) 2011. *Commonwealth Listing Advice on* Sternula nereis nereis *(Fairy Tern).* Canberra, Australia: Department of Sustainability, Environment, Water, Population and Communities.

VEEN, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern (*Sterna S. sandvicencis* Lath.). *Behaviour* Supplement 20: 1–201. doi:10.2307/30039178

WARD, M.P., SEMEL, B., JABLONSKI, C. ET AL. 2011. Consequences of using conspecific attraction in avian conservation: A case study of endangered colonial waterbirds. *Waterbirds* 34: 476–480. doi:10.1675/063.034.0410

WEIDINGER, K. 1998. Effect of predation by skuas on breeding success of the Cape Petrel *Daption capense* at Nelson Island, Antarctica. *Polar Biology* 20: 170–177. doi:10.1007/s003000050293

WILSON, E.C., HUBERT, W.A. & ANDERSON, S.H. 1991. Nocturnal roosting by Interior Least Terns early in the nesting season. *Nebraska Bird Review* 59: 42–43.