The influence of predation on the location and design of nests

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5.1 Introduction

For many species the risk of predation is ever-present and natural selection favours those individuals that employ behaviours that minimize the risk of predation (Caro 2005). Natural selection exerts strong selective pressures on birds during the breeding season when a predation event not only results in the loss of eggs or the offspring, which reduces reproductive success, but may also result in the death of the attending adult birds. Moreover, the risk of predation can also have a number of non-lethal effects on breeding birds that are probably underestimated compared with the direct effects. Indeed, many birds show an array of behavioural and physiological changes in response to the risk of predation, which often have important influences on the breeding biology of the birds (reviewed by Cresswell 2008). Consequently, there are strong selective pressures on the behaviours of the adult birds (reviewed by Lima 2009; Chalfoun and Schmidt 2012), but also on the location and design of nests. While all birds lay eggs they exhibit much variation in the location and design of nests. However, nests are multi-functional structures and other factors may determine their location and design (reviewed by Mainwaring et al. 2014a; Chapter 4).

In this chapter, we consider the effects of predation on nest location and design. The location of nests is defined in terms of their placement with respect to topography, micro-scale habitat, orientation, height, vegetative cover, and occurrence of other nests. Meanwhile, the design of nests is defined in terms of their building materials, shape, and size. We will also consider how nest ecology is determined by avoidance of predation and how it interacts with other selective factors, such as the requirement to act as a sexual signal, to reduce the impact of parasites or to create a suitable microclimate for offspring growth. Finally, we will indicate areas where further research attention should be focussed.

5.2 Factors affecting nest location

The location of nests varies greatly between species (Skutch 1976; Collias and Collias 1984; Hansell 2000). For example, a variety of seabirds nest on cliff ledges overlooking the world’s oceans whilst species such as oilbirds (Steatornis caripensis) nest inside caves. A huge range of passerines build their nests in trees, bushes, and vegetation close to the ground, ranging from species such as Australian ravens (Corvus coronoides) nesting in trees, Eurasian reed warblers (Acrocephalus scirpaceus) nesting in reeds, and grey catbirds (Dumetella carolinensis) nesting in woodland understory vegetation. Elsewhere, a variety of owls, raptors, woodpeckers, and passerines nest in tree cavities. Meanwhile, gamebirds nest in well-concealed locations within tall grasses and other vegetation at ground level whilst waders either build minimal nests or lay their eggs on the bare ground in no nest or just a scrape. These include pectoral sandpipers (Calidris melanotos) nesting on arctic tundra and Eurasian dotterels (Charadrius morinellus) nesting on alpine plateaux (Hansell 2000).

5.2.1 Topographical features

Birds select nest sites not just according to landscape and vegetation features but also in relation to local topographical features, such as slopes (Newell and Rodewald 2011). Such variation over relatively large scales might be more important at nest sites with little or no vegetation, as in ice-free Antarctic areas. Adelie penguin (Pygoscelis adeliae) colonies are positioned at locations within the landscape that provide benign microclimates with low risks of flooding (Moczydlowski...
1986, 1989). There is a general trend for ground-nesting birds to select slopes rather than flat areas as places on which to nest. Nests of water pipits (Anthus spinoletta) tended to be on east-northeast facing slopes in the Austrian and Swiss Alps where they provided shelter from prevailing winds which, in turn, resulted in greater fledgling production than nests on west-southwest facing slopes (Bohm and Landmann 1995; Rauter et al. 2002). Meanwhile, northern harriers (Circus cyaneus) clearly preferred nesting on north-west facing slopes in Scotland although this did not increase their breeding success (Redpath et al. 1998). This may be because the benefits were accrued directly by the adults as was the case in great bustards (Otis tarda) that preferentially nested on slopes orientated to the south-east that provided incubating females with protection from the cold north-westerly winds (Magana et al. 2010). Eggs and chicks of Atlantic puffins (Fratercula arctica) were less vulnerable to predatory gulls (Larus spp.) on slopes as they were less frequently displaced to burrow entrances by panicked take-offs of adults (Nettleship 1972).

Other species prefer to nest on flat areas, although they tend to be those that lay their eggs directly onto bare ground rather than in short vegetation. European golden plovers (Pluvialis apricaria) nesting on flat areas had significantly higher rates of survival than conspecifics nesting on slopes, which was probably due to predators being less visible from the latter (Whittingham et al. 2002). Meanwhile, mountain plovers (Charadrius montanus) prefer to nest almost entirely on flat areas perhaps as an adaptation to heavy rains since this would reduce the chances of nests being subjected to heavy run-off (Graul 1975).

5.2.2 The orientation of nests

Many studies have quantified the orientation of open cup nests built within short vegetation on the ground. Most of these quantify the orientation of either the nest entrance or the nest cup in relation to a nearby object such as a tuft of grass or a large stone. Studies provide scant evidence that the nest orientation influences their risk of being predated. Gillis et al. (2012) used artificial nests to show that the height of surrounding vegetation was the most important factor determining the location of nests as it simultaneously provided a suitable microclimate for offspring development and protected the nest contents against predators. Creation of a suitable microclimate seems to determine the orientation of open cup nests within short vegetation on the ground. Illustratively, many empirical studies report that birds breeding in relatively cool environments orientate their nests away from prevailing winds (Sidis et al. 1994; Hoekman et al. 2002; Burton 2006; Mallord et al. 2007; Long et al. 2009; Robertson 2009). Birds breeding in relatively warm or even hot environments orientate their nests away from the hot midday sun (Yanes et al. 1996; Hartman and Oring 2003; Tieleman et al. 2008). A systematic review of the subject by Burton (2007) concluded that at lower latitudes in the northern hemisphere, the requirement for shade from the hot sun resulted in the majority of nests facing northwards. Most nests at mid-latitudes face eastwards, probably reflecting a compromise between thermal benefits in the early morning and shade in the afternoon. At higher latitudes most nests face southwards in order to face the sun during the majority of the day (Burton 2007). The limited data available from the Southern Hemisphere conform to these general patterns (Mezguida 2004).

Thus, nest orientation does not appear to be random. When Lloyd and Martin (2004) experimentally changed the orientation of chestnut-collared longspur (Calcarius ornatus) nests by removing vegetation and providing artificial shade, nestlings grew more slowly in nests whose orientations had been altered compared with those in control nests that were kept in their original orientations. This confirmed that nestling growth was causally linked to variation in nest microclimate arising from nest-orientation preferences towards the south-east that resulted in high midday temperatures, suggesting that these preferences were not adaptive with regard to nestling growth. We need to consider in greater detail how nest orientation in relation to wind and sun is influenced by the configuration of the local terrain (Sutter 1997; Lloyd et al. 2000). Nest orientation may not always be important in determining nest microclimates or in some cases birds may be prevented from optimal nest orientation. For example, the orientation of saltmarsh sparrow (Ammmodramus caudacutus) nests is restricted by tidal conditions and prevailing winds that cause grasses to lie in one direction, which constrains the orientation of nest entrances (Greenberg et al. 2006). Moreover, perpendicular orientation of nest openings towards prevailing winds may reduce the dissipation of offspring and adult odours, although this hypothesis remains untested (Conover 2007).

The orientation of nests within tree canopies has been studied to a lesser extent than those on the ground, but similar findings emerge. There is a tendency for open nests to be orientated towards the sides of trees that best shelter them from prevailing winds (Martin and Roper 1988; Viñuela and Sunyer 1992; Summers et al. 2002; Rae and Rae 2013), or excessive sun in warmer
environments (Rae and Rae 2013), although not in all cases (Glück 1983). For cavity nests, a review of 16 studies involving 19 species across 11 families revealed that nine studies (56%) found that cavity-entrance orientation was not important during nest-site selection. By contrast, four (25%) found the opposite, and the remaining three (19%) provided evidence both for and against its importance (Rendell and Robertson 1994). Cavity entrances might be simply orientated away from the rest of supporting vegetation rather than to specific compass directions (Zwartjes and Nordell 1998).

Empirical studies provide some, but by no means consensual, support for nests being orientated to avoid prevailing winds or insolation. Such benefits from nest orientation may be indirect because they impact on the behaviour of incubating adult birds. Incubating mountain plovers tend to face away from the sun during the heat of the day and spend much time standing over the nest with raised feathers thus providing shade (Graul 1975). However, it was postulated that such behaviours may result in increased nest detectability to predators (Augustine and Skagen 2014). Incubating Adelie penguins consistently face towards strong winds resulting in reduced levels of vigilance, which makes the colony more vulnerable to attacks from South Polar skuas (Stercorarius spp.) approaching from the opposite direction (Young 1994a). However, our understanding of parental behaviours in relation to the orientation of nests remains poor and further studies could usefully examine if compensatory behaviours occur.

5.2.3 Nesting substrate in ground nests

In those species that lay their eggs directly on bare ground, it has been suggested that background matching reduces the risk of predation (Sánchez et al. 2004; Lovell et al. 2013; Chapter 12). For example, studies of waders nesting on beaches with pebbles have shown that the presence of egg-sized stones may enhance background matching (Cohen et al. 2008; Colwell et al. 2011). Stones may confer additional protection if predators fail to recognize real eggs amidst a backdrop of distracting egg-like objects (Stoddard et al. 2011). Moreover, greater mismatches between the colouration of eggs and surrounding stones resulted in higher levels of predation than nests with close matches (Solís and de Lope 1995; Blanco and Bertellotti 2002; Figure 5.1). Apart from background matching, crypsis

![Figure 5.1](image-url)
could be enhanced also through visual diversity of egg colouration within a clutch (Lloyd et al. 2000).

There are, however, inevitably trade-offs between maximizing heat reflectance to improve egg microclimate and minimizing the conspicuousness of nests containing eggs to predators (Mayer et al. 2009; Saalfeld et al. 2012). Both stone curlews (Burhinus oedicnemus) and Kentish plovers (Charadrius alexandrinus) nest on substrate with sparse amounts of short vegetation. When researchers experimentally removed camouflaging nest material from their nest sites, the birds replaced material rapidly (Solís and de Lope 1995; Szentirmai and Székely 2002). This suggests that such material has a functional role in crypsis and far from nests being simple, they may well be constructed to reduce the risk of predation.

5.2.4 Substrates for burrow and cavity nests

Many species nest in burrows and cavities and the selection of an appropriate substrate may be fundamental to a successful breeding attempt. For example, when they are excavating tunnels in soil banks in which to breed, sand martins (Riparia riparia) prefer to burrow into compacted soil to avoid entrance holes collapsing and thereby entrapping eggs, nestlings, or adult birds (Heneberg 2009). European bee-eaters (Merops apias) prefer to burrow in fine-grained sedimentary substrates while common kingfishers (Alcedo atthis) prefer highly compacted substrates (Heneberg 2013).

Hole-nesting species choose to nest in cavities that can either be in living or dead trees, with the latter often showing significant decay and thus containing more potential nesting cavities. Primary hole-nesting species often excavate cavities in dead trees as the wood is softer and hence, easier to excavate. However, secondary hole-nesting species are unable to excavate their own cavities and so rely on cavities that are created by decay over many years or excavated by primary hole-nesting species. Consequently, secondary hole-nesting species are often reliant on such species for breeding opportunities and without them, they must wait for cavity formation through damage from decay or lightning strikes (Cockle et al. 2011). However, studies show that marsh tit (Poecile palustris) nests in dead wood and old woodpecker (Dendrocopos spp.) holes are predated more frequently than those constructed in living wood and holes of non-woodpecker origin (Węsławski 2002). Hence, whilst primary hole-nesting species are able to nest in the safest locations as they can excavate their nests at preferred sites, secondary hole-nesting species have to nest where they can find a cavity, which may result in higher rates of nest predation.

5.2.5 Vegetation as nesting substrate

Vegetation provides structural support for nests and camouflage against detection by predators. While the importance of vegetative concealment is well recognized (see section 5.2.9), less attention has been paid to the role of species composition of nest-supporting or concealing vegetation. For example, while birds are well-adapted to concealing their nests in native trees and shrubs, Borgmann and Rodewald (2004) found nest predation rates to often be higher for nests in exotic shrubs than those of conspecifics nesting in native shrubs, although an opposite effect has also been reported (Schmidt et al. 2005). In temperate environments, there is a well-documented pattern of birds choosing to nest in deciduous trees and shrubs with increasing frequency as spring progresses and the amount of vegetation available to conceal nests increases (Morton et al. 1993; Ludvig et al. 1995). Nevertheless, birds choosing nest sites might discriminate even among similar plant species, as in the case of oak (Quercus spp.) trees within a mixed-oak forest (Newell and Rodewald 2011). Furthermore, yellow-faced honeyeaters (Lichenostomus chrysops) nesting in dioecious plants (Coprosma quadrifida) only nested in non-fruiting male plants. When artificial nests were placed in both fruiting and non-fruiting plants, nest predation rates did not differ between them (Boulton et al. 2003). On the other hand, lower predation on artificial nests placed in mistletoe (Amyema spp.) compared to eucalypt (Eucalyptus spp.) trees might explain the frequent use of this nesting substrate by Australian birds (Cooney and Watson 2008). This highlights the need for manipulative experiments to disentangle the effects of parental behaviour and nest-site traits per se.

Some species attempt to minimize the risk of predation by nesting in thorny vegetation which provides both a physical and visual barrier to predators. Thorny vegetation decreases incidents of predation by various snake species on baya weaver (Ploceus philippinus) nests (Quader 2006). When the perceived predation risk was experimentally increased using audio playback, female song sparrows (Melospiza melodia) built their nests in denser, thornier vegetation (Zanette et al. 2011). These studies suggest that individuals nesting in thorny vegetation are selected for, but further studies would confirm whether this behaviour is widespread.
For those species whose nests are located in more open parts of trees or bushes, patterns and types of branches are also likely to influence nest predation rates, because they may provide crypsis for the eggs, chicks, and attending adults. Tawny frogmouths (Podargus strigoides) placed their nests in rough, flaky-barked tree species and on open mid-branch sites with no foliage, where the birds’ plumage and posture resembled the colour and form of branches (Rae and Rae 2013). Other studies have shown that nesting success increased with thickness of the supporting branch (Quader 2006; Newell and Rodewald 2011), suggesting that structural support was more important than accessibility to climbing predators. Moreover, a multispecies study provided little evidence for ‘branch matching’ across 25 species producing lichen-bearing nests (Hansell 1996). As with other aspects of nest-site selection in relation to nest substrate, there are too few studies for us to make any major conclusions.

5.2.6 Factors affecting nest accessibility

Birds attempt to minimize the accessibility of their nest sites to predators by nesting in inaccessible locations such as on cliff ledges. However, such nest sites can potentially be accessed by avian predators and so further selection takes place at such sites to reduce accessibility even further. For example, the risk of predation for thick-billed murres (Uria lomvia; Gaston and Elliot 1996) and cape petrels (Daption capense; Weidinger 1998) was higher for those birds nesting on wide cliff ledges on which avian predators are able to alight than for those nesting on narrower cliff ledges. A similar pattern of predation emerged in nests of common murres (Uria aalge) which were inaccessible to predatory gulls when on narrow ledges, but eggs were exposed to higher risk of accidental displacement during nest defence on narrow ledges (Gilchrist and Gaston 1997).

Weather conditions also influence patterns of predation in addition to cliff topography and in this case when wind speeds were sufficiently forceful, gulls were able to hover adjacent to the nests and take eggs or chicks (Gilchrist and Gaston 1997). Moreover, nests of Antarctic petrels (Thalassarche antarctica) that were in more sheltered locations on rocky slopes suffered lower levels of predation but benefits of shelter were traded off against costs of meltwater flowing directly on to nests more frequently (Varpe and Tveraa 2005).

Some species nest underground in burrows where accessibility, among other factors, influences the risk of predation. The height of nest entrances was a significant predictor of egg loss in Magellanic penguins (Spheniscus magellanicus; Stokes and Boersma 1998) and the length of tunnels was positively correlated with daily nest survival rates in burrowing owls (Athene cunicularia; Lantz and Conway 2009). However, the risk of predation is not the only determinant of nest location in burrowing birds because the characteristics of the soil are also important. Sand martins nesting in burrows on river banks preferentially located their burrows in the upper third of the bank to minimize the threat of flooding and access to ground predators from below (Heneberg 2013). The nests that best survived were also at least 20–50 cm below the top of the bank, preventing inundation of rainwater and attacks from predators from above (Heneberg 2013). Manx shearwater (Puffinus puffinus) burrows are located in coastal areas and vary in their susceptibility to flooding. Males that nested in burrows that flooded in one year moved burrows in the following year whereas males that bred in dry burrows in one year tended to breed in the same burrows in the subsequent year (Thompson and Furness 1991). Pallid swifts (Apus pallidus) nesting in rock cavities have to balance the risk of flooding in deeper cavities with the risk of overheating in more exposed sites (Penloup et al. 1997). Favourable thermal conditions inside nesting burrows might even relieve parent crab plovers (Dromas ardeola) from incubation duties, thus providing benefit in terms of increased foraging and vigilance for predators (Marchi et al. 2015).

Hole-nesting birds suffer lower rates of predation than open cup-nesting species (Martin 1993a) but birds still choose nest locations that offer the most protection from predators with the entrance diameter and wood hardness being among the most important factors (Wesolowski 2002; Paclík et al. 2009). Red-cockaded woodpeckers (Picoides borealis) not only choose cavity location, but also modify the surface of the trunk. They excavate resin wells and remove loose bark around their nesting cavities in living pine (Pinus spp.) trees so as to resist predatory attacks from climbing snakes trying to access nests (Delotelle and Epting 2007). The pattern of nest-site use by marsh tits reflects security of cavities of different origin (Wesolowski 2002). Cavities situated in living trees and those with small entrances often meet requirements for both predator-resistance and favourable microclimate (Paclík and Weidinger 2007; Maziarz and Wesolowski 2013; Chapter 4).

Nests protected by water are particularly successful because many mammalian predators cannot access them. Survival rates of common pochard (Aythya ferina) nests increased along a wetland gradient (Figure 5.2; Albrecht et al. 2006). Nests of prothonotary warblers (Protonotaria citrea) were increasingly protected from
rates will decrease with nest height. However, a multi-
species comparative analysis of predation rates among
vegetation strata that controlled for habitat type
showed that the above prediction only held in open
grassland habitats (Martin 1993b). However, in wood-
lands predation was the lowest for ground nests and
highest for shrub nests (Martin 1993b). Such broad pat-
terns are less clear in cavity nesters, although within a
guild of cavity-nesting species in Arizona, species with
lower nest heights had lower nesting success (Li and
Martin 1991). Nevertheless, at a within-species level,
predation clearly partly drives nest height. Orange-
crowned warblers (Vermivora celata) on a mainland site
exposed to avian and mammalian predators nested at
ground level while conspecifics that were introduced
to an island where avian predators were absent nested
off the ground and away from mammalian predators
(Peluc et al. 2008). The above example demonstrates
that different classes of predators often exert opposing
selective pressures with respect to nest height. If
these effects are compensatory rather than additive,
the total predation will be independent of nest height
(Remeš 2005a). Such predator-specific effects, whether

Figure 5.2 The mean survival (with 95% confidence intervals) of natural and artificial common pochard (Aythya ferina) nests along a wetland
gradient from dry ‘terrestrial’ areas with minimal water nearby through to wet ‘island’ areas surrounded by water. Note that natural nests are
represented by grey bars and artificial nests are represented by white bars. Nest survival was extrapolated to 32 days, i.e. the period of laying and
incubation, from daily survival rates; sample size varied from 20 to 93 nests per group. Reproduced with permission from Albrecht et al. (2006).

raccoons (Procyon lotor) by increasing water depth
(Hoover 2006). However, Brewer’s blackbirds (Eupha-
gus cyanocephalus) that nested in bushes located within
water traded off their inaccessibility to land predators
with reduced levels of nest concealment, because
flooded vegetation lost more leaves than that rooted
in dry land (Furrer 1975). Nesting over water does not
always reduce rates of nest predation and, in fact, a
study of large-billed gerygones (Gerygone magnirostris)
in Australia showed that it may incur increased costs
from more frequent flooding events (Noske et al. 2013).
Consequently, further studies are required to examine
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suspected or documented (Söderström et al. 1998; Conkling et al. 2012; Sperry et al. 2012; Vanderwerf 2012), may account for the inconsistent results of empirical studies. Some studies have shown that higher nests are predated less frequently than lower nests (Burhans et al. 2002; Antonov and Atanasova 2003; Yeh et al. 2007), others have found the opposite (Hatchwell et al. 1999; Prokop 2004), and some have shown nest height to have negligible influence on nest predation rates (Hirsch-Jagobson et al. 2012; Latif et al. 2012).

Although the majority of studies suggest some link between predation rate and nest height, predation must surely not be the predominant selective factor determining nest heights in all ‘study systems’. For example, more elevated nests are more often usurped by raptors (Prokop 2004) and those nests built in less stable branches are more vulnerable to damage from, and displacement by, strong winds (Bijlsma 1984). Moreover, microclimate in nests located higher and on the periphery of trees and shrubs differs markedly from nests within the corpus of vegetation. Under laboratory conditions open cup nests of Australian birds experienced increased heat loss when exposed to windy conditions (Heenan and Seymour 2012). In cooler temperate environments, pinyon jays (Gymnorhina cyanocephalus) nested in more exposed and higher sites during cold weather because solar radiation reduced the energetic costs to nesting females (Marzluff 1988). Nest heights of mountain white-crowned sparrows (Zonotrichia leucophrys oriantha) decreased as spring progressed and declining snow cover enabled ground nesting but there was no effect of nest height on predation rates (Morton et al. 1993). Even small differences in height above ground might expose nests to opposing selective pressures. For example, meadow pipit (Anthus pratensis) nests placed relatively higher within grass tufts were more vulnerable to predation but incubating females had lower energetic expenditures as the nests were less damp (Halupka 1998). Similarly, the risk of flooding also declines with nest height in large-billed gerygones (Noske et al. 2013), but higher nests of Savi’s warblers (Locustella luscinioides) and various sparrows (Melospiza spp.) are predated more frequently with declines in nest concealment as vegetation becomes more sparse (Aebischer and Meyer 1998; Greenberg et al. 2006). Other species have adapted aspects of their reproduction to the threat of flooding, with one study showing that saltmarsh sparrows time their reproduction to avoid especially high tides, while seaside sparrows (Ammodramus maritimus) avoid flooding by nesting in taller vegetation (Gjerdrum et al. 2005; Chapter 15).

5.2.8 Nest concealment by vegetation

We expect nests concealed by vegetation to be predated less because of restricted transmission of visual (Santisteban et al. 2002), auditory (Haff and Magrath 2011) and olfactory cues (Conover 2007) to potential predators. Borgmann et al. (2013) reported seasonal variation in the risk of nest predation associated with foliage density. Hatchwell et al. (1996) reported higher nest predation rates at exposed, rather than concealed, common blackbird (Turdus merula) nests, and the same was true in a study of artificial nests in an aviary study (Santisteban et al. 2002).

Studies that experimentally manipulate the vegetative concealment of nests are rare. While some have shown that the experimental concealment of nests influences predation in the expected direction (Stokes and Boersma 1998; Latif et al. 2012), others have not (Howlett and Stutchbury 1996). Such inconsistent findings are currently difficult to explain but, as above, the effects are probably predator-specific and density-dependent and nest concealment may be traded off against other factors. For example, the potential-precite hypothesis (Martin and Roper 1988; Martin 1993a) proposes that the probability of a predator finding stationary prey, such as eggs or nestlings, should decrease with increasing numbers of unoccupied potential sites that must be searched. By contrast, the total-foliage hypothesis (Martin and Roper 1988) predicts that predation rate should decrease with the total volume of vegetation containing nests. A habitat manipulation study provided unequivocal support for the former hypothesis as birds chose nest patches containing both greater total foliage and potential nest-site density, but only the latter factor significantly influenced nest predation rate (Chalfoun and Martin 2009). Apart from density of potential nest sites, the effect of nest concealment was modulated by the density of active conspecific nests. Well-concealed nests of Eurasian reed warblers are generally less often parasitized by the common cuckoo (Cuculus canorus), which is also an egg predator. However, when the density of available warbler nests was low, cuckoos increased their searching effort to the degree that concealment had no beneficial effect on the rate of parasitism (Jelinek et al. 2014).

Predation on nest-attending adults is potentially an important source of mortality (Reidy et al. 2009). Hence, nest concealment may also be traded off against the degree of visibility that adults afford themselves as they incubate eggs or brood chicks but also remain vigilant against predators (Götmark
et al. 1995). Accordingly, great bustards select sheltered nest sites with good visibility of surroundings (Magana et al. 2010), while other ground-nesting birds also prefer generally open habitats (Keyel et al. 2013), even those habitats that are disturbed by a combination of herbivores, fire, and drought (Augustine and Skagen 2014). In rock ptarmigans (Lagopus muta) concealed sites were less often detected by predators but were more risky for incubating females that were less able to escape from predators once they had been detected (Wiebe and Martin 1998). Two sorts of evidence support the above correlational data. First, experimentally restricting the view of incubating birds from their nests delayed detection of approaching predators and they were more likely to succumb to predation on covered than on exposed nests (Amat and Masero 2004). Secondly, selection of nest sites might reflect tolerance to stress, where bold individuals should select concealed sites at the expense of lowered chances of escape from predation (Sellmann et al. 2014). Yet another situation where low nest concealment might be an advantage is in the advertisement of its likely low profitability (Galligan and Kleindorfer 2008; see section 5.3.2), which may discourage predators from closer inspection of obvious or already discovered nests (Schmidt 1999).

We have much to learn about the adaptiveness of nest concealment and the lack of progress may be due to simplistic approaches in investigations to date. Most studies use a single metric of habitat or behaviour as a measure of predation risk, but this overlooks a focal species’ capacity for compensation in other behaviours (Weidinger 2002). Illustratively, studies have shown that there is sometimes no effect of nest concealment on predation rates at natural nests, but there was a positive effect when such nests were baited with plasticine clutches at which there was no parental activity. Thus, incubating adults probably compensated behaviourally for poor concealment of natural nests (Cresswell 1997; Remeš 2005b). On the other hand, any parental activity may disclose the nest location to potential predators thereby increasing predation rates (Smith et al. 2012), although not all studies have detected such an effect (e.g. Pope et al. 2013). Finally, visual components of nest concealment may also be traded off against non-visual ones, such as olfactory cues (Lehman et al. 2008; Conover et al. 2010). This rather speculative final point reflects our poor knowledge of how concealment acts as an important determinant of nest predation rates in birds. Further research in this area is needed urgently.

5.2.9 Nest sites and density dependence

Nest predators may select for nest-site diversification among co-occurring bird species via density-dependent foraging amongst predators. Hence, nest locations that disrupt the perceived nest density by predators may reduce nest losses from predation (Martin 1988). Indeed, those individuals within a species using nest sites that overlap with co-existing species experienced higher predation rates, thus suggesting nest-site partitioning among species (Martin 1996). However, such an effect is not supported in all studies such as in the case of partitioning of nest sites among vegetation strata (Reitsma and Whelan 2000). Nest predation rates of cavity-nesting common goldeneyes (Bucephala clangula) were unaffected by the experimental addition of artificial nests simulating those of ground-nesting mallards (Anas platyrhynchos), despite both nests being commonly predated by pine martens (Martes martes). Hence, there was no apparent competition between nesting guilds or heterospecifics and no density-dependence in predation risk (Elmberg and Pöysä 2011). Nevertheless, Wada (1994) found that presence of nests of conspecifics determined nest predation rates in Oriental turtle doves (Streptopelia orientalis), with heights of neighbouring nests influencing predation risk more than the height of the focal nest itself.

In terms of density dependence the effects on nest predation are equivocal across studies. For example, there was no support for consistent effects of density dependence on predation rates of natural and artificial songbird nests (Schmidt and Whelan 1999). By contrast, predation rates on artificial and natural duck nests were not influenced by density dependence at the level of individual wetlands but there was stronger evidence for it at larger spatial scales (Gunnarsson et al. 2013; Ringelman et al. 2014).

5.2.10 The profitability of nest contents as prey

Nest predation rates may be strongly influenced by the foraging behaviour of predators and the proportion of nests within a search area that are active and thus contain prey in the form of eggs and/or nestlings. Thus, predators might abandon searching for eggs and/or nestlings if the majority of nests within a search area are empty (Schmidt 1999) and so it may be in the interests of birds to decrease the ratio of active:inactive nests. There are three ways in which birds can achieve this: 1) by building multiple nests themselves within a given breeding attempt; 2) by forcing the abandonment of
nests of neighbouring conspecifics and heterospecifics; and 3) through the accumulation of old nests.

Several species build multiple nests, including Australian reed warblers (Acrocephalus australis) and winter wrens (Troglodytes troglodytes). Nests built in addition to those in which eggs are laid are often thought to be part of sexual selection signalling the ‘quality’ of the builder (de Neve and Soler 2002) but they may also confuse predators (Hansell 2000). Whilst some studies have provided support for the anti-predator hypothesis of multiple nests (Leonard and Picman 1987; Watts 1987; Whitney et al. 1996; Noske et al. 2013), others have not supported this hypothesis (Metz 1991; Cavit et al. 1999; Berg et al. 2006), even when the number of inactive nests was experimentally increased (Dubois and Getty 2003). For multiple nests to dilute the ratio of active/inactive nests through accumulation, nests must last for more than one breeding attempt. Studies have shown that 74% of Eurasian blackcap (Sylvia atricapilla) nests remain undamaged post-breeding and are thus available for potential replacement nesting attempts during the same breeding season (Zielinski 2012). Over 90% of red-winged blackbird (Agelaius phoeniceus) nests survive between two successive breeding seasons (Erckmann et al. 1990). However, species such as the hair-crested drongo (Dicrurus hottentottus) sometimes destroy their nests to reduce future competition for nest sites (Li et al. 2009). Nevertheless, nests are often sufficiently durable to accumulate at least within a single year, which would predict predation rates decreasing towards the end of the breeding season (Schmidt 1999). This phenomenon is traditionally explained by changes in vegetation concealment and availability, or other prey for potential predators (Borgmann et al. 2013). Explicit tests of this idea are lacking and this field is thus open to further study.

5.2.11 Nest-site reuse

Birds may reuse nests from the previous breeding season. While this is advantageous in terms of time saving (Cavit et al. 1999) and having an intimate local knowledge of the breeding territory (Saunders et al. 2012), there may also be some disadvantages. For example, predators may remember nest locations from previous breeding attempts, both within and across seasons (Weidinger and Kočvara 2010) and ectoparasite load may increase over the lifetime of the nest structure (Chapter 8). Open cup-nesting species sometimes reuse old nests, preferably those that were previously successful (Styrsky 2005) or those in safe locations (Yeh et al. 2007). However, other studies reveal that nest reuse is rare (Cavit et al. 1999), has no effect on nest success (Antonov and Atanasova 2003; Jiménez-Franco et al. 2014), and only occurs when high-quality nest sites are in short supply (Redmond et al. 2007; Cancellieri and Murphy 2013).

Shortage of nest sites is prevalent in hole-nesting species (Hansell 2000; Mazgajski 2009; Cockle et al. 2011; Wesołowski 2012), with excavation of cavities being energetically and temporally expensive for primary hole-nesters (Wiebe et al. 2007). High-quality nest sites and their supply are then restricted in some cases for secondary hole-nesters. From this we can expect frequent reuse of existing tree cavities, in spite of potential costs in terms of ectoparasite exposure (López-Arrabé et al. 2012; Mazgajski 2013). Nestbox experiments suggest that absence of ectoparasites was a more important determinant of nest-site selection than indications of previous successful reproductive events (Stanback and Dervan 2001). However, marsh tits breeding in natural cavities reused holes more frequently after successful reproduction than after failure (Wesołowski 2006). Accordingly, most empirical studies show that there is no clear effect of the presence of old nests on nest-site selection of secondary hole-nesting species (reviewed by Mazgajski 2007), which might be facilitated by rapid decomposition of old nest material (Hebda et al. 2013). Nevertheless, suitability of tree cavities as nesting sites ultimately deteriorates with their age as a consequence of wood decay (Wesołowski 2012) and increasing predation risk due to long-term memory of predators (Mazgajski 2009).

Site fidelity is usually high in long-lived seabirds but even here change of nest sites is more frequent after breeding failure (Ollason and Dunnet 1988; Thibault 1994). Moreover, in colonially breeding black-legged kittiwakes (Rissa tridactyla) the breeding success of neighbours may influence site fidelity more than the birds’ own breeding experience (Danchin et al. 1998; Bled et al. 2011). Notable in this respect is the nest-site tradition in lesser grey shrikes (Lanius minor); most nests in successive years are built in the same or in neighbouring trees, but almost exclusively by different individuals. Hence, nest-site choice in this species is likely influenced by social information gathered from the presence of conspecifics and their breeding success (Kristin et al. 2007; Hoi et al. 2012). In summary, we know very little about the causes and consequences of nest reuse by birds and further studies could usefully examine the relative contributions of predation, parasitism, and conspecific attraction in determining the reuse of old nests.
Apart from reusing old nests, birds may use the presence of old nests of conspecifics as a cue for selecting new nest sites nearby (Safran 2004; Gergely et al. 2009; Ringhofer and Hasegawa 2014). However, high densities of old nests might not indicate suitable habitat as it may result from a high nest predation rate combined with a high rate of nestling. A bird’s ability to determine the fates of such old nests may be extremely limited, perhaps explaining why so many studies have failed to find support for old nests acting as such cues (Erckmann et al. 1990; Yahner 1993; Cavitt et al. 1999).

5.2.12 Responses to predators

There is strong selection on the anti-predatory behaviours of breeding birds (Lima 2009). Nest predation is such a critical determinant of fitness that assessment of predation risk is an important component of habitat selection (Mönkkönen et al. 2009). Prior to nest building, birds may assess the local abundance of avian predators through heterospecific eavesdropping (reviewed by Magrath et al. 2014). The local abundance of mammalian predators can be assessed through detection of their excrement in the environment by means of ultra-violet (UV) vision and/or olfaction (Eichholz et al. 2012; Forsman et al. 2013). Birds prospecting potential nest sites can detect chemical cues left by predators inside nest cavities (Amo et al. 2008; Mönkkönen et al. 2009).

Birds not only perceive predation risk but respond to it by choosing safer nest sites (Forstmeier and Weiss 2004; Roos and Part 2004; Eggers et al. 2006; Peluc et al. 2008; Latif et al. 2012) or by spacing out nests (Hogstad 1995). However, they may respond to habitat predictors of predation risk rather than to real presence of predators (Møller 1988). However, in unpredictable environments, breeding birds may lack sufficient cues to determine predation risk accurately but, instead, may have to rely on direct experience of predation (Chalfoun and Martin 2010a). Accordingly, birds can react after their nest contents have been predated by moving to build a nest in a safer location (Marzluff 1988; Haas 1998; Chalfoun and Martin 2010b; Kears and Rodewald 2013). However, not all studies have found such an effect (Howlett and Stutchbury 1996; Hatchwell et al. 1999; Kershner et al. 2004; Walk et al. 2004).

Humans can also be perceived as predators and disturbance can induce anti-predatory behaviours in birds. Great grey shrikes (Lanius excubitor) disturbed at the nest by researchers in one year increased their nest height the following year whereas undisturbed birds nested at the same height across both years (Antczak et al. 2005). Meanwhile, black redstarts (Phoenicurus ochruros) located nests in deeper cavities in the subsequent breeding season following human disturbance but nests remained at equivalent cavities across two years when not disturbed (Chen et al. 2011).

Taken together, the above evidence suggests that nest placement is a plastic trait that can develop with individual breeding experience and thus contribute to age-related improvement in breeding success (Horie and Takagi 2012). Although heritability of nest placement might be low (Yeh et al. 2007), nest height was shown to evolve in response to natural selection through novel predation pressure in an island environment (Figure 5.3; Vanderwerf 2012).

5.2.13 Presence of heterospecifics

Some species take advantage of breeding colonially, i.e. closeness and synchrony of breeding with neighbouring conspecifics (reviewed in Caro 2005). Other species sometimes preferentially nest close to other species and gain possible benefits by doing so. By associating with more aggressive species, often not restricted to the same taxa, birds seek protection from predators (reviewed in Quinn and Ueta 2008). In other cases birds simply exploit habitat created by other species or associate with their prey. For example, burrowing owls breed in black-tailed prairie dog (Cynomys ludovicianus) colonies where vegetation is kept short (Lantz and Conway 2009). Such interactions can be complex and require extensive research to elucidate their dynamics. For example, while breeding attempts of South Polar skuas (Stercorarius maccormicki) close to Adelie penguin colonies fail more often as a result of egg trampling by penguins and predation by conspecifics, they benefit from direct access to penguin eggs and chicks, suggesting that there may be an optimal distance for such heterospecific associations (Hagelin and Miller 1997). Thus, birds often, but not always, accrue benefits from nesting in association with heterospecifics. For example, predation rates on European pied flycatcher (Ficedula hypoleuca) nests were higher within, compared with outside, Ural owl (Strix uralensis) breeding territories, possibly because some smaller predators that do not directly threaten owl nests were attracted to the owls’ breeding territories (Morosinotto et al. 2012).

To nest in close association with protective species birds must adjust location of their nests. Thus, common wood pigeons (Columba palumbus) associated with Eurasian hobbies (Fulco subbuteo) build nests considerably...
higher and breed in synchrony with them compared to non-associated pairs (Bijlsma 1984). Savannah sparrows (Passerculus sandwichensis) nesting within gull (Larus spp.) colonies chose nesting microhabitats avoided by gulls (Wheelwright et al. 1997). Azure-winged magpies (Cyanopica cyanus) use nest sites that are less concealed by vegetation when nesting in association with Japanese sparrowhawks (Accipiter gularis; Ueta 1998). Finally, the costs and benefits of associations are likely to be context-dependent. An experiment with great tits (Parus major) and European pied flycatchers showed that birds nested in trees with ants only under increased predation risk, but otherwise preferred trees without ants (Haemig 1999).

5.3 Nest design

In addition to the location of nests, birds can also minimize predation risk through their appropriate design. The three primary ways in which nest design may exert influence are through: types of nest material used; the basic structure of nests; and the size of nests.

5.3.1 Nest materials

Birds use a wide diversity of nest materials and, whilst their function is comprehensively discussed in Chapter 4, here we discuss some of the more unusual nest materials and their role in minimizing predation risk. For example, some species use snake skin as a nest material, despite snakes being predators of many avian species (Borgo et al. 2006; Clucas et al. 2008). There is mixed empirical support for the hypothesis that snake skin reduces predation risk. Medlin and Risch (2006) found a lowering of predation risk at nests with snake skins but they had no effect in artificial nests (Trnka and Prokop 2011). Some species use mammalian scat as nest material. Some plovers (Charadrius spp.) select nest sites that are closer to piles of dung than randomly selected sites (Graul 1975). Burrowing owls routinely

Figure 5.3 The number of elepaio (Chasiempis sandwichensis) nests on Oahu, Hawaii, that were predated/abandoned or were successful in relation to their height. The height of sequential nests built by individual birds did not change between 1996 and 2011 (inclusive), but the average height of nests increased by 50% suggesting that predation risk selected for higher nests. Note that predated/abandoned nests are represented by white bars and successful nests are represented by black bars. Reproduced from Vanderwerf (2012) with permission from John Wiley & Sons.
collect dry mammalian manure and scatter it around their nesting burrows (Smith and Conway 2011), perhaps to provide olfactory camouflage of eggs and chicks from predators (Levey et al. 2004). Common waxbills (Estrilda astrild) regularly use carnivore scat as nest material that lowers predation risk compared to control nests without carnivore scat (Schuetz 2005). The presence of faecal sacs in common blackbird nests had no effect on nest predation rates (Ibáñez-Álamo et al. 2014), but future research should examine the role of olfactory cues in predation events (Conover 2007). This is especially in light of a study of European rollers (Coracias garrulus) that confirmed that birds can ‘smell the fear’ of their offspring (Parejo et al. 2012). In addition, Canestrari et al. (2014) showed that carrion crow (Corvus corone) nests parasitized by great spotted cuckoos (Clamator glandarius) experienced lower predation due to smelling of repellent secretions from cuckoo chicks.

Feathers are another commonly used nest material and they are usually considered to create a suitable microclimate for offspring development (reviewed by Mainwaring et al. 2014a; Chapter 4). However, the experimental addition of feathers to nests resulted in higher nest predation rates than for control nests (Møller 1987). More broadly, it has been suggested that predation risk is the selective pressure that prevents all species from using feathers. This is because species suffering relatively low nest predation rates, such as hole-nesting species and those nesting above ground level, use feathers as nest material to a much greater extent than species suffering higher levels of predation (Møller 1984).

Many hole-nesting species incorporate green plant material into nests and they normally replenish them daily during the incubation and nestling stages (reviewed by Dubiec et al. 2013). They contain volatile secondary compounds that are biocides of parasites and pathogens (Chapter 8), but they also sometimes play a role in sexual selection (Brouwer and Komdeur 2004; Tomás et al. 2013). Although their incorporation could serve many functions, we know only one study that has examined how (or whether) they influence nest predation: the addition of flowers to artificial nests had no effect on predation outcome (McGuire and Kleindorfer 2007).

During incubation in many bird species no adults are temporarily present at the nest, but some species cover eggs with nest material during incubation recesses. This behaviour is usually explained within the context of an improved nest microclimate for developing embryos but such a hypothesis has received little empirical support (Haftorn and Slagsvold 1995). Instead, several studies have shown that such behaviour reduces nest predation rates in open (Kreisinger and Albrecht 2008; Fast et al. 2010; Prokop and Trnka 2011) and possibly also in cavity nests (White and Kennedy 1997). Specific microhabitats, such as tree cavities, represent shared resource for cavity-nesting birds and other non-avian species. Rodents are major predators of cavity-nesting passerines (Adamík and Král 2008a, 2008b; Czeszczewik et al. 2008) and they sometimes even occupy such nests to their own ends to save time and energy in nest construction. However, the role of specific nest materials in such interactions remains unknown. This is seldom considered in studies of open nests but a study of common blackbirds suggested that usurpation of nests occurred by rodents for their own reproduction and as food stores (Tamarit et al. 2012).

Nest materials may also be used to modulate nest humidity; that is, a measure of water vapour retention within nests (Slagsvold 1989b; Deeming 2011b). Although nest materials are usually thought to influence nest microclimate, they might contribute also to olfactory concealment. Indeed, some studies have shown that environmental humidity controls olfactory cues received by predators with the best conditions for predators being cool and humid nights with low air movements (Conover et al. 2010). Accordingly, the predation rates of several birds varied in relation to climatic conditions. The daily survival rates of savannah sparrows nests were highest on cool and wet days (Stauffer et al. 2011). Wet weather conditions resulted in higher nest mortality in mountain plovers as a result of higher activity levels and enhanced olfactory sensitivity of predators (Dinsmore et al. 2002; Dreitz et al. 2012). Thus, predators are more efficient at locating nests under certain weather conditions such as high winds and high rainfall (Webb et al. 2012). However, Mainwaring et al. (2014b) found that nest design of common blackbirds that suffer from high losses from nest predation did not differ in relation to changes in spring precipitation. However, the location and design of nests are likely to vary in relation to weather-induced variation in the behaviours of predators and so further studies should examine these issues in greater detail.

Birds also use a variety of anthropogenic materials as nest materials and as the world is urbanizing (United Nations 2014), we might predict increased incorporation of such materials into nests in the future. Whilst there is a great deal of anecdotal evidence for such materials (see Chapter 4), their functions remain unclear (Igic et al. 2009). Sergio et al. (2011) showed plastics in the nests of black kites (Milvus migrans) were involved
in intraspecific signalling, but many more studies are required to examine such phenomena in more detail. However, anthropogenic materials are not always advantageous to birds with, for example, adult and nesting great grey shrikes becoming entangled in plastics incorporated in nests (Antczak et al. 2010), effects of which may cause massive mortality in seabirds under some circumstances (Votier et al. 2011). Meanwhile, house finches (Carpodacus mexicanus) line their nests with cellulose from smoked cigarette butts as it reduces the number of ectoparasites in nests but effects are not all beneficial. As the number of cigarette butts in nests increased, fledging success and immune responses of nestlings decreased, possibly due to their increased exposure to nicotine and other harmful substances (Suárez-Rodríguez and Macías Garcia 2014).

5.3.2 Nest structures

Nest structures vary greatly across bird species (Hansell 2000; Hansell and Deeming 2002; Chapters 3 and 4). Some nests have false structural components to deceive nest predators. Yellow-rumped thornbills (Acanthiza chrysorrhoa) build a lower domed nest where eggs are laid and an upper cup-shaped structure, referred to as the ‘false nest’. Artificial nests with false nests had significantly lower predation rates than those lacking such structures (Figure 5.4; Galligan and Kleindorfer 2008), indicating that such nest structures fulfil an anti-predation function. Acadian flycatchers (Empidonax virescens) build nests with ‘tails’ but nest predation rates were not associated with the prominence of such tails and so their purpose remains unclear (Master and Allen 2012). Although an attractive proposition, structures such as nest roofs provide benefits not only in terms of physical protection from predators, as is the case with the massive nests of magpies (Cyanopica and Pica spp.; Quesada 2007). Saltmarsh sparrows’ domed nests with intact roofs retained eggs during tidal flooding better than nests with experimentally removed roofs (Humphreys et al. 2007), suggesting that domes may protect eggs not just through minimizing nest predation. Consequently, our knowledge is rather incomplete as to how such nest structures influence nesting success. Yet, we are in no doubt that nest predation is one of the major factors selecting for specific nest structures and types.

5.3.3 Nest size

For visual predators nest size must largely determine prey detectability with larger nests expected to be detected more easily than smaller ones (Møller 1990a; Götmark 1992). Some observational studies have shown that larger open cup nests are predated more frequently than smaller nests (Gregoire et al. 2003; Antonov 2004), but such correlative results refer to combined effects of nest size, nest location, and parental behaviour. Nevertheless, experiments with artificial nests have shown that larger nests are predated more frequently when placed in artificial locations (López-Iborra et al. 2004) or when nests of different sizes are

![Figure 5.4](image-url) The number of yellow-rumped thornbill (Acanthiza chrysorrhoa) nests that were predated in relation to the presence of false nests. Thornbills build nests comprising a lower domed section in which eggs are laid and an upper cup-shaped structure which is a false nest. Using artificial eggs, there were 15 nests in each treatment: ‘T1’—eggs in domed nests with false nests attached; ‘T2’—eggs in domed nests without false nests; and ‘T3’—eggs in false nests attached to a dome. Length of exposure: ‘Early’ (0–16 days) or ‘Late’ (17–34 days). Early exposure is represented by grey shading and late exposure by white shading. Reproduced from Galligan and Kleindorfer (2008) with permission from John Wiley & Sons.
swapped between original locations (Figure 5.5; Møller 1990a; Biancucci and Martin 2010). Experimental eggs directly attached to branches rather than within nest structures survived better than eggs placed in nests (Götmark 1992). Even for those species that build nests on the ground in the form of stone piles, the presence of more stones might be costly in terms of increased nest predation (Weidinger and Pavel 2013). Reductions in nest size are likely constrained by the need for protective nest structures or balanced by opposing selection on nest size (Fargallo et al. 2001).

The positive relationship between the size of nests and the rate of predation is unsurprising given that larger open cup nests provide larger visual targets for visual predators, while larger nests inside cavities decrease the ‘danger distance’ between the cavity entrance and nest contents (Mazgajski 2009; Kaliński et al. 2014). However, other studies of open cup-nesting species have found no evidence for nest size influencing nest predation rate (Lent 1992; Hatchwell et al. 1996; Palomino et al. 1998; Herranz et al. 2004; Suárez et al. 2005). In an experimental study Weidinger (2004) studied nests of different species that constructed nests of different size and exchanged them between locations, showing that nest location was more important than nest size in determining nest predation rate.

Thus, while individual breeding birds may be trading off nest size against location, other factors may also be influencing nest size. The requirement for adequate structural support is the primary selective influence on nest size in Australian cup-nesting species (Heenan and Seymour 2011) although one study showed this may not necessarily always be the case (Palomino et al. 1998). This latter result may be explained by nest size co-varying with microhabitats resulting from physical constraints imposed by the architecture of nest-supporting vegetation (Lent 1992), or from environmental conditions across broad latitudinal gradients (Møller 1984; Mainwaring et al. 2012, 2014b).

Clearly, there is a research opportunity to examine the trade-off between building a sufficiently large nest that is well-insulated against one that is sufficiently small to minimize predation risk (Mainwaring et al. 2014a). Empirical studies to date have generally examined the relationship between nest size and predation rates in a rather oversimplified manner. Future research must
examine how nest size interacts with nest location and parental behaviours to advance our understanding of the evolution of nest size of birds.

5.4 Summary and conclusions

Although all birds lay eggs, they show a wide diversity of nest locations and designs ranging from eggs laid on the bare earth by plovers (Charadriidae) through to small open cup nests built by warblers (Sylviidae) and huge stick constructions built by storks (Ciconiidae). Here, we have shown that such diversity is influenced by the risk of predation (Caro 2005). However, nests are multi-functional structures (Mainwaring et al. 2014a) and we discuss how provision of a suitable microclimate for offspring development and, to a lesser extent, their role as sexual signals and in combating parasites and pathogens, also explain such diversity.

We have a reasonable understanding of the determinants of variation in nest location and design, but there are four main avenues where further research is warranted. First, nests are multi-functional structures and studies have generally only considered a single function (e.g. minimization of predation risk) in isolation. For example, many studies have experimentally increased nest size and then monitored nest fate in terms of presence/absence of predation events without considering whether there are confounding variables. Non-building individuals of some species feed offspring more intensely at larger nests in response to the elevated investment of the building bird in the reproductive event. In this case, parental provisioning behaviours may disclose the nest location to predators.

Secondly, a wide range of methodological approaches are currently used to quantify nest location, nest design, and nesting output, and they can introduce bias into research findings. For example, studies focus on those species most accessible to researchers and at sites where birds are present at the highest densities. Moreover, studies have often used artificial nests but we know little about how much they differ from ‘natural’ nests that they are trying to mimic. For example, there are strong concerns that the absence of parents from artificial nests means that they do not realistically mimic a ‘natural’ reproductive event. Possibly the most serious weakness of nest predation studies to date is the anonymity of nest predators, but this can be recorded using video technology (Ribic et al. 2012). However, the anticipated anti-predator function of various nest traits is not only traded off against other functions, but the predators themselves might exert opposing selective pressures due to the diversity of their foraging modes.

Thirdly, we are using ever more sophisticated technologies to quantify the size and location of nests but we understand little about the biases associated with such approaches. For example, open cup nests are often quantified in terms of their location within a bush and their size in terms of their outer diameter when measured in a laboratory. However, the vegetation within the bush may be crucial in terms of nest dimensions and function, and is likely to change over the course of the breeding season in temperate regions. Such seasonal adjustments in nest characteristics must be considered and the data analyzed as time-dependent covariates.

Finally, studies should also consider how changing environmental conditions may force birds to alter nest location and design. For example, as ambient temperatures increase in arid regions of the world, nests may need to be located in shaded areas or the parents may need to build further sheltering structures to shade nest contents from direct sunlight. Such aspects are considered further in Chapter 6.

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