Vines and canopy contact: a route for snake predation on parrot nests

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Summary

Ornithologists have hypothesized that some tropical forest birds avoid snake predation by nesting in isolated trees that do not have vines and canopy contact with neighbouring trees. Here we review two complementary studies that support this hypothesis by demonstrating (1) that an abundance of vines and an interlocking canopy characterized Jamaican Black-billed Parrot *Amazona agilis* nest-trees that failed due to chick loss, presumably to snakes, and (2) that such trees were used preferentially by an arboreal snake congeneric to the snake implicated in the parrot losses. Evidence strongly suggested that losses of nestling Black-billed Parrots were due in substantial part to predation by the Jamaican (yellow) Boa *Epicrates subflavus* (Boidae). Studies of the closely related *Epicrates inornatus* on Puerto Rico revealed that trees used by boas had more vine cover and more crown or canopy contact with neighbouring trees than did randomly selected trees. Moreover, the boas had relatively large home ranges and were most active during March to July, which corresponds with the breeding season of parrots as well as other bird species. We suggest that nest failure due to snakes may be reduced in endangered bird species through isolating the nest-tree by eliminating vines and canopy contact with neighbouring trees and shrubs and by placing barriers on the nest-tree trunk.

Introduction

Ornithologists have long recognised that predation of eggs or nestlings is a major cause of nest failure for many bird species (Ricklefs 1969, Martin 1992, Newton 1993). In tropical America, Skutch (1985) observed that snakes were the primary predators of avian nests, destroying more nests than all other predators combined (see also Weatherhead and Blouin-Demers 2004, Thompson and Burhans 2004, Robinson *et al.* 2005). To reduce the risk of such predation, Snow (1976) suggested that some species of tropical forest birds nest in isolated trees with no vines or canopy contact with neighbouring trees. The adoption of smooth-surfaced trees or barkless snags may also provide some degree of protection from predation by climbing snakes (Withgott 1996). For many bird species, adaptive responses in nest-site selection are an expected result of the natural dynamics of predator–prey interactions, although predation threats are not the only factor influencing nest-site selection. When endangered bird species are involved, however, understanding how their predators hunt and access prey can be crucially important for developing effective conservation actions.

In this paper, we review the results of two field studies, one of which examined the breeding biology and causes of nest failure of Black-billed Parrots *Amazona agilis* in Jamaica (Koenig 1999, 2001) and the other of which investigated the movements and habitat use by Puerto Rican Boas *Epicrates inornatus* in Puerto Rico (Wunderle *et al.* 2004). Although the studies were conducted on different Caribbean islands, there are taxonomic and ecological similarities that led us to compare our results. In Jamaica, the major predator of nestling Black-billed Parrots is the

Jamaican (or yellow) Boa *Epicrates subflavus*, a species closely related, and ecologically similar, to the Puerto Rican Boa (Tolson and Henderson 1993). On both islands, we compared the vegetative structural traits of trees: on Jamaica, the traits of trees with successful versus depredated parrot nests; on Puerto Rico, the traits of trees used by boas versus random trees. Our comparisons found some congruity between vegetative structural traits of trees in which parrot nests were depredated and trees used by Puerto Rican Boas. These results not only provide insight into how snakes access trees used by nesting birds, but suggest ameliorative actions that may reduce the risk of snake predation on the nests of intensively managed endangered species. This is particularly relevant to management of critically endangered species such as the Puerto Rican Parrot *Amazona vittata* for which potential chick losses to Puerto Rican Boas are a serious concern (Snyder *et al.* 1987).

Case studies

Black-billed Parrot Amazona agilis

The Black-billed Parrot is one of two species of Amazon parrot endemic to Jamaica. It is the smallest species in the genus *Amazona* (26 cm in length and $173 \pm$ SD 11 g at fledging) and occurs primarily in mid-elevation (100–600 m) moist and wet closed broadleaf forest on limestone (Koenig 1999). As secondary cavity-nesters, Black-billed Parrots require forests for suitable nest-sites. Formerly common throughout much of Jamaica, by the mid-1970s the species had become rare in eastern Jamaica (Cruz and Gruber 1981). The parrot is still locally common in Cockpit Country, an area encompassing approximately 25,000 ha of karst 'hay stack' hills covered in primary and secondary moist and wet evergreen forest. This region is also the only location where both Black-billed Parrot and Yellow-billed Parrot *A. collaria*, Jamaica's second endemic Amazon parrot, occur sympatrically in large numbers. Approximately $8,500 \pm 1,500$ territorial pairs of Black-billed Parrots are estimated from Cockpit Country (Davis 2002). The species is listed as Vulnerable by IUCN (Snyder *et al.* 2000) and appears in Appendix II of CITES.

Black-billed Parrot breeding biology was studied from 1995 through 1998 at elevations of 100–400 m in the northern region of Cockpit Country (for details see Koenig 1999, 2001). Briefly, from 1996 through 1998, 63 nesting attempts were monitored. A nesting attempt was defined as a pair initiating egg-laying. Territorial pairs exploring and defending potential nest-cavities but failing to lay eggs were not included in the final count. Full-day observations from camouflaged hides were conducted to document parrot behaviour. For nests that were safe to climb to, nestlings were accessed from either the cavity entrance or through an access door cut at the base of the cavity. Periodic checking of nestlings allowed collection of data on nestling growth and mortality, notably the timing and causes of nest failure.

Physical features of cavities, trees and the surrounding habitat were quantified to distinguish between habitat variables associated with nest success and failure. Measured vegetative characteristics with the potential to facilitate predator movements included: tree health (snag or live tree); canopy connectivity; and presence of vines on the tree trunk. The connectivity of the nest-tree canopy to neighbouring trees was estimated with a binomial scoring on the cardinal ordinates N, S, E, W, where a score of 4 represented full connectivity and 0 represented complete isolation of the nest-tree. Vine coverage on the trunk of the nest-tree was qualitatively assessed as 'none', 'few' (1 or 2 vines) or 'many'. These were subsequently collapsed into binomial categories of vines absent (0) or present (1) as there was no significant difference between the presence of a 'few' or 'many' vines (Tukey HSD = 0.951).

During the 1998 breeding season, a predator control experiment was conducted. Initially, randomly assigned nest-trees were 'girthed' with nylon monofilament netting with 1.9 cm (3/4 inch) mesh (Forestry Suppliers, Jackson, MS), similar to designs used elsewhere to protect cavity-nesting birds from snake predation (Eichholz & Koenig 1992, Neal *et al.* 1993). When it

became apparent that the mesh netting neither trapped nor deterred predators, nest-trees were then girthed with 1 metre high galvanized sheet metal. The top 10 cm of the metal was smeared with petroleum jelly in hope of identifying tracks of predators, but the petroleum liquefied in the warm ambient temperatures (20–32°C). Although efforts at the time of the field research were not directed towards quantifying bark characteristics, a feature that may facilitate a predator's ability to climb, qualitatively the five species of trees that were girthed varied from the smooth-barked *Adenanthera pavonina* to the very rough-barked *Persea americana*.

Puerto Rican Boa *Epicrates inornatus*

The Puerto Rican Boa is endemic to Puerto Rico and occurs in a variety of habitats from sea level to 400 m (Reagan 1984). It is a medium-sized snake, with a maximum snout–vent length (SVL) of 1,860 mm (Schwartz and Henderson 1991). The boa is chiefly a nocturnal forager and its diet consists of a diversity of prey items, including invertebrates, lizards, rats, bats and birds (Reagan 1984, Rodríguez & Reagan 1984, Rodríguez-Duran 1996, Wiley 2003). The species was believed to be very common in the late nineteenth century (Schwartz & Henderson 1991) but declined in abundance and distribution following a period of intense deforestation in Puerto Rico in the late 1800s (US Fish and Wildlife Service 1986).

Telemetry studies were conducted in the subtropical wet forest zone *tabonuco* (*Dacryodes excelsa*) forest at 65–438 m elevation) of the Luquillo Experimental Forest (LEF) in eastern Puerto Rico from 1996 through 2001 to examine the movements and habitat use by boas (for details see Wunderle *et al.* 2004). Radio transmitters were surgically implanted into the body cavities of 24 snakes to monitor their movements and habitat use. Telemetered boas were located twice weekly (once during daylight and once in evening darkness) and 18 boas were followed for approximately a year. Snake locations were geo-referenced and vegetation characterized in a 16 m diameter circle centred on the tree used by immobile boas. Vegetation traits of 93 trees used by nine boas were compared with 71 randomly selected trees to identify the vegetation traits that distinguished trees used by boas from random trees. The following vegetation characteristics were measured in each circle: central tree diameter at 1.5 m height (dbh), tree height, number of free vines, number of attached vines (attached closely to the bole), understorey shrub density, mean percentage canopy cover over the circle, and canopy continuity. Canopy continuity with neighbouring trees was estimated on a scale of 1 to 4: a rank of 1 indicated the central tree had a crown fully contiguous (100%) with surrounding crowns; 2 was a crown which was highly contiguous (75%); 3 was a crown which was moderately contiguous (50%); and a crown ranked 4 had little or no continuity (< 25%) with neighbours. In addition, the point quarter method (pqm) was used for the nearest broadleaf tree distance, nearest free vine distance and nearest free vine diameter.

Comparative results of case studies

Black-billed Parrot *Amazona agilis*

Of 63 nesting attempts by Black-billed Parrots, 35 (56%) failed before fledging at least one chick (Koenig 2001). Causes of chick mortality varied, but predation of nestlings accounted for over one-third of total nest failures (Figure 1). For 13 nests, predation of nestlings was the principal cause of failure: 10 nests experienced 100% predation of nestlings and three nests experienced brood reduction of neonates followed by predation of older nestlings. At two additional nests, partial predation occurred, but each nest fledged one chick. At one final site, one nestling disappeared at 21 days of age. Its sibling was alive at 47 days of age but was gone when the nest was checked at 50 days of age. With a mean nestling period of 54.6 ± 2.2 days, it was likely that this chick was taken by a predator. However, to be conservative, this nesting attempt was excluded from the current analysis. Also excluded so as to be conservative with our analyses
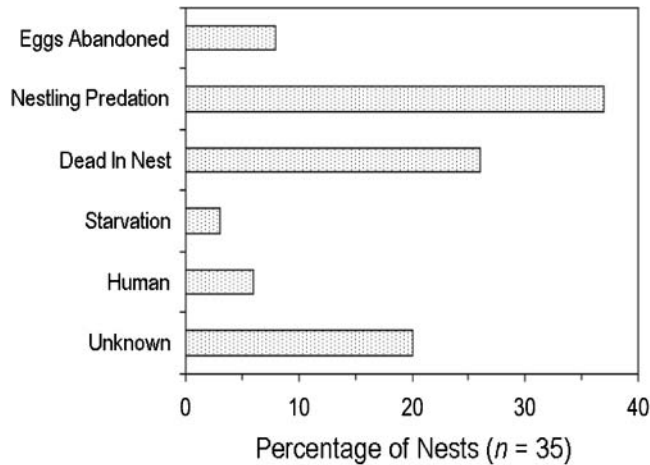
Figure 1. Percentage of Black-billed Parrot nest failures attributable to different factors for nest-sites that failed before fledging at least one chick in Cockpit Country, Jamaica, 1996–1998. The figure is based on data presented in Koenig (2001).

were two nests for which fledging or late-stage predation could not be determined reliably. Fledging is asynchronous and the complete disappearance of the clutches raises suspicion of a predation event. As a further note, one prolific pair fledged three chicks annually, including during the pilot season of 1995, and adopted the same tree each year; we only incorporated the characteristics of this nest once to prevent over-representation in the dataset. For the analyses summarized here, if a nest suffered any degree of predation ($n = 15$), it was classified as 'depredated'.

Two structural features of nest-trees were associated with nestling predation: nests with vines on the trunk were more likely to fail (Mann–Whitney $U = 66.0$, $P = 0.007$), and as canopy connectivity increased to neighbouring trees, so too did the probability of predation (Mann–Whitney $U = 55.0$, $P = 0.004$; Figure 2). Although tree health was significant when all causes of nestling mortality were analysed (Mann–Whitney $U = 133.5$, $P = 0.05$), this characteristic was not significant for nests in which predation occurred (Mann–Whitney $U = 203.5$, $P = 0.14$; Figure 2). However, four of seven nests for which cause(s) of nest failure could not be determined were in snags, which were not safe to climb for regular monitoring.

Of eight active nest-trees girthed with metal sheeting, five were depredated in the early and middle stages of nestling development. Two of the three successful nests produced fledglings in previous years without any excluder devices on trees.

Strong direct evidence revealed that Jamaican Boas were predators of parrot nestlings. For instance, a boa was captured by Rudolf Diesel in an active Black-billed Parrot nest after the snake consumed two of the three chicks and the third chick remained perched precariously on the snake (Figure 3). Other evidence was found at a Yellow-billed Parrot nest, where leg bands of a fledgling parrot were found in a boa faecal pellet 3 m from the nest-tree along with a shed snake skin. This nest was used the following year by Yellow-billed Parrots and failed again during the nestling period, with a shed snake skin found at the cavity entrance.

Other evidence was circumstantial but led to the supposition of snake predation rather than avian or mammalian predation, including: (1) eggs were never broken, nor did abandoned eggs have etched marks from beaks or teeth; (2) eggs were never taken, even when hatched siblings were depredated; (3) mammal faeces were never found in nests; and (4) the depth of most parrot nests (mean 198 cm) would probably prohibit access by most avian predators (e.g. Jamaican Crow *Corvus jamaicensis*). An example of factor (2) was observed in 1997. Two of three
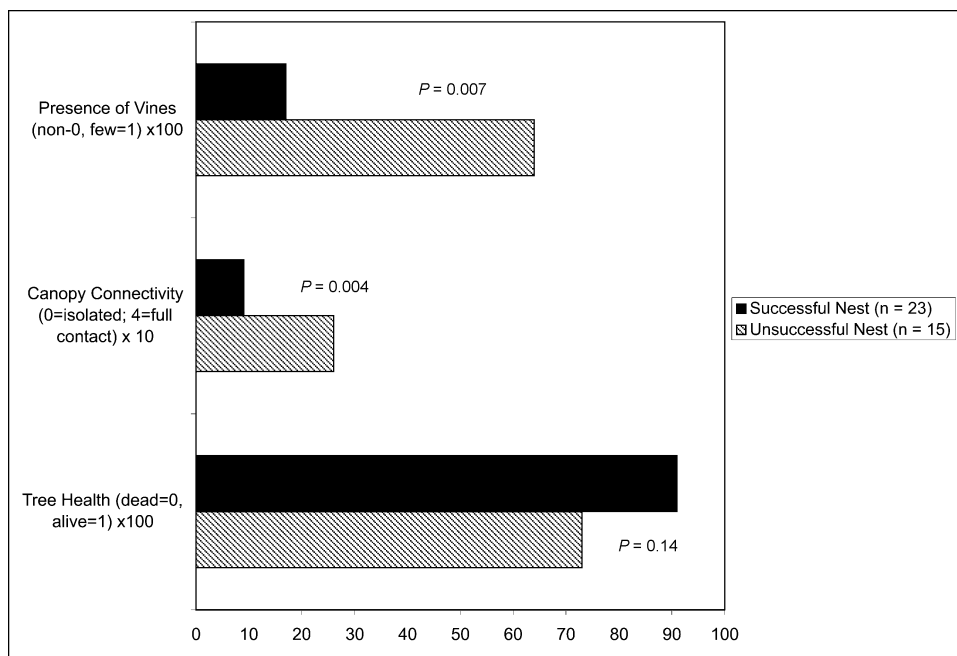
Figure 2. Characteristics of Black-billed Parrot nests in which successful nests differed significantly from depredated nests based on 33 nest-sites adopted for use in 38 breeding attempts in Cockpit Country, Jamaica, 1996–1998. Successful nests are defined as nests in which at least one chick fledged. Nests which failed due to factors other than predation of nestlings are not included. The figure is based on Koenig (1999), where details of the statistical analysis are provided.

Black-billed Parrot eggs had hatched, with neonates being several days old. The third egg was pipped and expected to hatch the following day. A full-day nest watch was undertaken, only to be abandoned at noon owing to the extremely agitated behaviour of the adults and their failure to enter the nest-cavity to tend chicks and egg; the female apparently was flushed from the cavity overnight as she did not emerge from roosting, but rather, flew into the nest stand with her mate at 08h00. Upon return the following day, it was discovered that the two oldest chicks had disappeared from the nest. The nestling in the pipped egg had hatched within hours of the nest check, its primary down still wet with splotches of egg yolk. Within 2 days, this third nestling was depredated. The adults remained in the nest stand for several days, but they made no attempts to enter the cavity. In further support of factor (2), during feeding trials, which included quail eggs (presented both warmed above ambient temperature and 'cold' at ambient temperature) and other live prey items, Puerto Rican Boas crawled over and around eggs but did not consume any eggs (Wunderle unpubl. data; see also Marini and Melo 1998).

Puerto Rican Boa *Epicrates inornatus*

As found in other *Epicrates* species (Tolson and Henderson 1993), Puerto Rican boas were opportunistic in their use of habitat (Wunderle *et al.* 2004). Boas were found in a diversity of locations from terrestrial (percentage of fixed locations 34.9% + SD 25.9; includes below-ground fixes) to arboreal sites (52.8% + 30.1 fixes) and other locations of lesser importance (e.g. streams, buildings). However, boas did demonstrate selectivity in arboreal sites, with the broadleaf trees

Figure 3. Black-billed Parrot chick sitting on a Jamaican Boa that has previously consumed two nest mates in May 1999 in Cockpit Country, Jamaica. Photograph by Rudolf Diesel.

in which they were located differing from randomly sampled broadleaf trees in a number of traits (Figure 4). Trees used by boas differed from random trees in that they had larger diameter trunks, were taller, were closer to other broadleaf trees, were surrounded by a higher density of understorey vegetation and had a lower percentage canopy cover. More importantly, trees occupied by boas also had more crown contact with neighbouring crowns than random trees, had more vines (both attached and unattached to the trunk) and the nearest vines were closer to the trunk and had larger diameters than vines on randomly sampled trees.
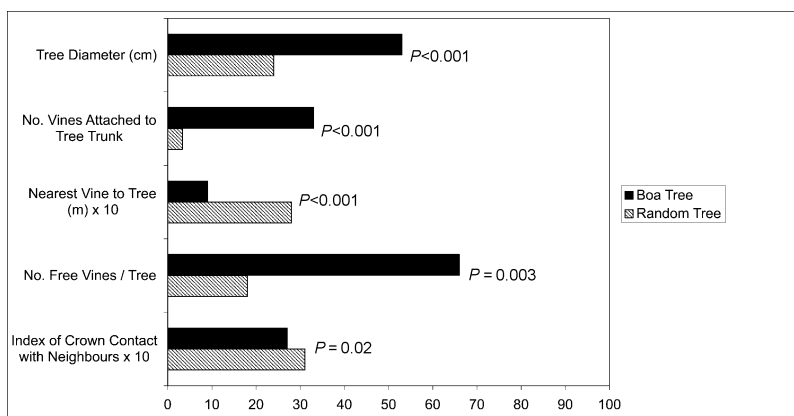

Figure 4. Characteristics of trees occupied by Puerto Rican boas that differed significantly from random trees based on 0.02 ha circular plots centred on broadleaf trees in which boas were located with radio telemetry in the Luquillo Experimental Forest, Puerto Rico. Measurements were made on 93 trees used by nine boas and 71 randomly selected trees, as summarized with an explanation of the statistical analysis in Wunderle *et al.* (2004).
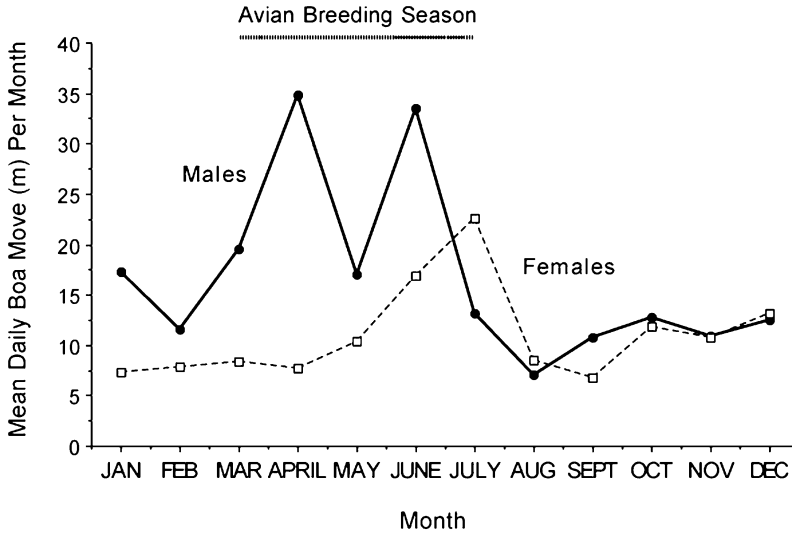
Figure 5. Change in mean daily movement (m) per month for nine male and nine female Puerto Rican Boas tracked with radio telemetry for approximately 1 year each in the Luquillo Experimental Forest, Puerto Rico. The figure is based on Wunderle *et al.* (2004) and shows the duration of the avian breeding season in the same forest based on Waide (1996).

Puerto Rican Boas varied seasonally in their movement patterns (Figure 5). Males were especially active from April though June, which corresponds to the boa mating period. The increase in activity suggested that males actively searched for females during this time, as is common for many solitary snakes (Gibbons and Semlitsch 1987). Female movement peaked in July, which may have been related to the need to increase foraging to sustain embryo growth or to shift to environments appropriate for gestation and parturition (e.g. exposed terrestrial sites for thermoregulation). This April through July peak in boa movements also corresponds approximately to the breeding seasons for some prey in the study area, a period when foraging boas may encounter a more abundant and vulnerable (i.e. immobile young) prey. For example, juvenile black rats *Rattus rattus* are most abundant in the *tabonuco* forest from April to August (Weinbren *et al.* 1970). Similarly, the peak of avian breeding occurs in March to July (Waide 1996). Correspondingly in Jamaica, the breeding season of Black-billed Parrots occurs from late March through mid-July and the Jamaican Boa's reproductive cycle (and presumably movement cycle) is reportedly similar to that of the Puerto Rican Boa, with a parturition period of August–September (Cruz and Gruber 1981). Thus the peak of boa movements in moist and wet forests on the two islands coincides with the breeding period of potential prey.

Despite their greater mobility, male Puerto Rican Boas did not differ significantly from females in the size of their annual home range. The median annual home range size for 18 boas (nine males, nine females) was 8.5 ha (95% adaptive kernel method; range 2.0–105.5 ha) and 5.6 ha (95% minimum convex polygon method; 0.7–68.1 ha). Fidelity to a specific location within the annual home range was usually low, at least for the 1 year duration of the telemetry study for each boa. For example, during movements by nine males, 13% of the locations were revisited once, 4% of the locations were revisited twice and 1% of the locations were revisited on three occasions. Similarly for females, 16% of locations were revisited once, 6% twice, 1% three times and 2% of the locations were visited four times. Thus not only are the annual home ranges of Puerto Rican Boas relatively large, but the boas move, and probably search, widely in these areas, at least in the *tabonuco* forest of the LEF.

Discussion

The structure of an animal's environment often has a strong influence on its reproduction and survival. For Black-billed Parrots, the adoption of a nest-tree free of vines, lianas and other climbing vegetation, or a tree isolated from the surrounding canopy, appears to offer greater protection against predation by Jamaican Boas. Supporting these observations, Puerto Rican Boas preferentially use trees with vine cover and an interlocking canopy. In a similar study of habitat use of the congeneric Virgin Island Boa *Epicrates monensis*, habitats with interlocking canopies were used preferentially for foraging on *Anolis* lizards (Chandler and Tolson 1990). Crown connectivity enables arboreal snakes to move more easily through the canopy in search of prey items. Vines can also be important to snakes for gaining access to trees either from the ground or from other trees and for providing cover for foraging and resting (Shine & Fitzgerald 1996, Fitzgerald *et al.* 2002). Vines may be particularly useful for snakes in environments with smooth-barked trees. For example, the climbing ability of Black Rat Snakes *Elaphe obsolete* decreases sharply with the smoothness of tree trunks (Withgott 1996). The preference of several temperate-zone species of woodpeckers for smooth, barkless snags for nesting was interpreted by Withgott (1996) as an adaptive response to the threat of predation by the semi-arboreal Black Rat Snake. We have similarly noted the preferential use of isolated smooth-barked *Bursera simaruba* trees in Mexico by a variety of nesting bird species, including kiskadees, flycatchers, becards and orioles (Enkerlin-Hoeflich unpubl. data). From observations of snakes attempting to climb this tree species, it appears extremely difficult for them to maintain a 'grip' with their ventral scales, and the snakes fall to the ground after ascending less than 2 metres.

That Puerto Rican Boas utilized trees larger (dbh) than randomly available suggests special risks for cavity-nesting species, including parrots, given the increased availability of suitable nest-cavities in larger trees (Snyder *et al.* 1987). Bigger trees also provide larger branches to support heavier snakes (Henderson and Winstel 1995), are more likely to have vine cover (Brokaw *et al.* 2002) and have larger crowns, thereby increasing the likelihood of contact with neighbouring crowns (Plummer 1981, Tolson 1988, Henderson and Winstel 1995).

Although our studies were not carried out on the same islands, the results provide unique insights into the interactions between *Amazona* parrots and *Epicrates* boas on both Jamaica and Puerto Rico. In Jamaica, Black-billed Parrot nests were located across a gradient of habitat types, from isolated trees in pasture, through edge habitat to interior forest. Nest-trees in edge habitat were noted particularly for their abundance of vines, which probably benefited from increased sunlight in this habitat. Further, only 26% of nests (*n* = 30) located in regenerating edge habitat successfully fledged at least one chick. In contrast, isolated trees in agriculture/pasture locations had a success rate of 61% (*n* = 28). Similarly, 60% (*n* = 5) of nests in moderately disturbed interior forest successfully fledged at least one nestling. Of the nests that failed, 50% experienced predation in regenerating edge, compared with 21% in agriculture/pasture and 0 in the interior forest (Koenig 1999). Assuming adult survival rates are comparable to those of other insular Amazon parrots (Snyder *et al.* 1987), reproductive performance of Black-billed Parrots in regenerating edge habitat might not be adequate to maintain a stable or increasing population size (i.e. this represents sink habitat), whereas nesting success in the interior forest and in pastures appears sufficient for maintaining a healthy population (i.e. source habitat; Koenig 1999).

Other Amazon parrots have displayed similar successful use of isolated trees in pastures. In Tamaulipas, Mexico, Red-lored Parrot *Amazona autumnalis*, Yellow-crowned Parrot *A. ochrocephala oratrix* and Green-cheeked Parrot *A. viridigenalis* have shown a remarkable avoidance of nesting in patches of forest (minimum 50 m × 50 m patch of remnant native vegetation) and shelterbelts (strips of native vegetation > 50 m long and < 50 m wide) despite a high abundance of cavities that appeared suitable for use. Based on cavity availability in a 525 ha study area, 27 parrot nests were expected in forest habitat, but only two nests were observed (Enkerlin-Hoeflich 1995). In marked contrast, 32 nests (instead of an expected 23) were found in

open pasture (average nine trees with dbh > 27 cm ha^{-1}) and 42 nests (compared with an expected 27) in wooded pasture (average 16 trees ha^{-1}). Snake predation in forest patches was hypothesized to explain the strong preference for pastures. Where it was possible to determine predator identity, Indigo Snakes *Drymarchon corais* accounted for 25% of nestling mortality, followed by skunks (probably *Spilogale putorius*) accounting for 19% (Enkerlin-Hoeflich unpubl. data). These two predators may have contributed further to nestling mortality as 32% of predators were ''unknown'' at the Tamaulipas study area. Although vine coverage was not quantified in this study, in three fully documented cases of snake predation the presence of vines and broken branches on the trunk of the nest-tree facilitated climbing by snakes, providing a 'ladder' at least two-thirds of the distance to the cavity entrance. It is also interesting to note that in three cases of Green-cheeked Parrot predation, the nestlings were killed, but not eaten, by Indigo Snakes, presumably because the chicks were too big for the snake to consume (Enkerlin-Hoeflich *et al.* 1993).

Although it is unknown whether Jamaican Boa abundance varies across the habitat gradient, the boa is common in the Windsor study area. Since 1995, 44 Jamaican Boas have been captured, marked and released by the Windsor Research Centre (Koenig unpubl. data). While encounter probabilities may be higher in edge habitats compared with the interior owing to the fact that edges are frequented more regularly by farmers, the results of the Black-billed Parrot study suggest that boa abundance and accessibility of parrot nests to boas may be higher in forest edge than interior. Boa prey such as birds are often more abundant in forest edge than interior because of abundant resources such as flowers and fruits associated with higher light levels of the forest edge relative to interior understorey (e.g. Feinsinger 1976, Restrepo *et al.* 1999). In addition, forest edges associated with human activities might support higher densities of non-native rats (*Rattus* spp.) than forest interior. Assuming higher prey densities along forest edge than interior, it is reasonable to expect predators, such as boas, to concentrate in edges. Indeed, *Epicrates* boas are known to concentrate in sites with high prey densities, such as are found at entrances of bat caves (Rodríguez and Reagan 1984, Rodríguez-Duran 1996). In addition, the structure of edge habitats (e.g. dense understorey, vines and lianas, an interconnected canopy of trees of the same stage class) may facilitate more efficient searching of trees by boas. Finally, the higher levels of sunlight in edge habitat may promote more efficient thermoregulation by boas and, consequently, higher densities, particularly of gravid females (Weatherhead and Charland 1985).

High nest predation rates by boas and other snakes may have contributed to the nesting behaviour and vigilance traits of some parrot species. For example, Black-billed Parrots were extremely wary in the nest stand, hesitating or aborting attempts to tend to nestlings when human observers were not well camouflaged and motionless (Koenig 2001). Such vigilant behaviour is also seen in Amazon parrots on the mainland, where predation by snakes occurs (Enkerlin-Hoeflich *et al.* 1993). The behaviour of these parrots is in sharp contrast to the Amazon parrots on Dominica, Imperial Parrot *Amazona imperialis* and Red-necked Parrot *A. aurusiaca*, which show little regard for observers and are not believed to suffer from snake predation (Koenig unpubl. report). The range of the native *Boa constrictor* overlaps extensively with that of Dominica's parrots (Lazell 1964), but adult snakes possessing a mouth gape large enough to swallow these large Amazon parrots would be too large and heavy to move and forage efficiently in the canopy (Rodríquez-Robles & Green 1996, J. Lazell, verbally).

Patterns of nestling attendance by adults may also be influenced by predation risk, with the associated costs and benefits to both offspring and parents (Montgomerie and Weatherhead 1988, Brunton 1990). Black-billed Parrot females cease continuous daytime brooding of nestlings when the oldest chick is about 10 days of age (Koenig 2001). At this time, they also terminate nocturnal brooding, which will reduce the time period during which a female is exposed in the cavity to the risk of nocturnal predation. Anecdotally, we know of one female that was flushed from her nest-cavity during incubation, amidst a flurry of squawks, at 04h00. The eggs remained unbroken, but the female did not return to her nest that season.

In Puerto Rico, female parrots have recently made a dramatic shift in their roosting behaviour. Prior to 2000, females roosted with their chicks for nearly the duration of the nestling period (Snyder *et al.* 1987, Wilson *et al.* 1995). It was speculated that the remnant population's recent (1940s) restriction to the high elevations of the LEF, a region with low boa density, relaxed the selective pressures against lengthy brooding or roosting periods (Snyder *et al.* 1987). However, since 2000, females have been ceasing nocturnal brooding when chicks are 10–16 days old (T. White *in litt.*), their predicted age of attaining effective homeothermy. This change in behaviour was observed in wild birds, pre-dating the recruitment of captive-reared birds into the breeding population by several years. It also pre-dates the usage of closed-circuit infrared video monitoring in nest-cavities (White and Vilella 2004). Increasing attention is being given to Black Rats *Rattus rattus* as potentially important nocturnal predators, as at least one event of rat predation, not merely scavenging of a failed nest, has been documented (Engeman *et al.* 2006).

The ability to alter roosting behaviour so rapidly may prove extremely important for Puerto Rican Parrots. This species, which at one time dwindled to 13 individuals in the wild, has been the focus of intensive management for more than 30 years (Snyder *et al.* 1987, Wiley *et al.* 2004). Despite substantial recovery efforts, the population remains small and restricted in range in the LEF. Predation by Puerto Rican Boas has not been a cause of nestling mortality in recent years, mainly because the parrots currently nest at elevations (500–700 m; White and Vilella 2004) above the core range of boas. However, plans to re-introduce parrots to the karst region (known locally as *mogotes*) of north central Puerto Rico near Rio Abajo (Wiley *et al.* 2004) will return the parrots to a region with relatively high densities of Puerto Rican Boas (Puente Rolón 1999). The Puerto Rican Parrot historically occurred in the *mogotes* with boas, and it is likely that the characteristics and possibly even the intensity of boa predation on chicks there will be similar to the boa predation on parrot chicks in the ecologically similar Cockpit Country of Jamaica.

Management implications

These studies suggest that elimination of vines and crown contact with neighbouring trees may hinder snake access to nest-trees. For endangered cavity-nesting birds, such as the Puerto Rican Parrot, it may become necessary to trim vegetation to preclude access to nest-trees by snakes. Vines can be cut to reduce access to a nest-tree and tree crowns trimmed so that the nest-tree crown is isolated from neighbouring crowns. The appropriate isolation distance will depend upon the gap-bridging abilities of the target predators. In Puerto Rico, for example, a gap of 1.5 m is likely to be adequate to prohibit canopy access of boas to nest-trees as this species has not been observed crossing gaps greater than 0.5 m. Direct access to the nest by snakes can be hindered by a barrier placed around the tree trunk, although experimentation may be required to identify the appropriate barrier design. For example, experimentation with metal sheeting on tree trunks to hinder climbing Jamaican boas was not successful, possibly because irregularities in the metal sheeting associated with encircling the tree (e.g. pounding edges of the metal to be flush with the bark) or with the heads of nails used to hold the metal in place may have provided the boas with enough corrugation to grip the metal (G. Rodda *in litt.*). Others have tried galvanized steel bands and a sticky petroleum-based gel as trunk barriers to snakes in conjunction with vegetation trimming without success (Aguon *et al.* 1999). Electrical and hardware cloth barriers on the tree trunk and vegetation clearing were successful in eliminating access to nests of the critically endangered Mariana Crow *Corvus kubaryi* by the Brown Treesnake *Boiga irregularis* on Guam (Aguon *et al.* 1999). Nylon netting can also be an effective trunk barrier as demonstrated by a 68% increase in nest success of Red-cockaded Woodpeckers *Picoides borealis* following netting placement on nest-tree trunks (Neal *et al.* 1993). While nylon netting was not used successfully in Jamaica, it was partially effective at parrot nests in Mexico, with three snakes netted during a 2 month period; another nest, however, was predated despite the netting. As a note of caution, particularly when the snakes themselves are threatened or endangered species, netting must be

checked regularly to ensure that snakes or other non-target species do not perish. Indeed, the netting experiment in Mexico was terminated when a captured snake died.

To reduce the risk of nest abandonment by sensitive species, ''snake-proofing'' activities should be done in the non-breeding season for species that show high site fidelity to a traditional nest-site, or at night for species that do not roost in the nest at night (Aguon *et al.* 1999). If vegetation trimming is expected to cause too much disturbance to a nest-site, neighbouring trees can also be snake-proofed to isolate the nest stand. Finally, for some species, snake trapping may be necessary in addition to snake-proofing of nest-sites (Lokemoen and Woodward 1993, Aguon *et al.* 1999).

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