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Does rock disturbance by superb lyrebirds (*Menura novaehollandiae*) influence habitat selection by juvenile snakes?

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Abstract: Vertebrates that destroy or disturb habitats used by other animals may influence habitat selection by sympatric taxa. In south-east Australian forests, superb lyrebirds (*Menura novaehollandiae*) displace soil, leaf litter and rocks during their daily foraging activities. We investigated whether superb lyrebirds disturb small sandstone rocks that endangered broad-headed snakes *Hoplocephalus bungaroides* and common small-eyed snakes *Cryptophis nigrescens* use as diurnal thermoregulatory sites. To estimate the frequency of lyrebird rock disturbance, and to assess whether lyrebirds also attack small snakes, we placed 900 plasticine snake replicas under stones on rock and soil substrates along transects on three sandstone plateaux. Because juvenile snakes must select retreat sites that simultaneously allow them to thermoregulate and minimize predation risk, we quantified the thermal environments underneath stones on rock and soil substrates. During the 6-week experiment, animals disturbed rocks on soil substrates twice as often (16.9%) as rocks lying on rock substrates (8.2%). Disturbed rocks were significantly smaller and lighter than undisturbed rocks on both substrates. Lyrebirds were the major agents of disturbance, and attacked 40% of snake models under disturbed rocks. Rocks on soil substrates conferred the greatest thermal benefits to snakes, but both species of snake avoided these microhabitats in the field. Instead, juvenile snakes selected rocks on rock substrates, and sheltered under stones that were too heavy for superb lyrebirds to disturb. By disturbing rocks over millennia, superb lyrebirds not only have shaped the physical landscape, but also may have exerted strong selection on habitat selection by sympatric snakes.

Key words: biopedturbation, disturbance, predation risk, thermoregulation, trade-off.

INTRODUCTION

Disturbance is a fundamental force that influences the structure and function of ecosystems (Wootton 1998). Although it is well known that large-scale abiotic disturbances (fires, floods, hurricanes) strongly affect biological diversity (Huston 1994), smaller-scale biotic disturbances caused by vertebrate digging and burrowing (biopedturbation) can also influence the spatial heterogeneity and diversity of many landscapes (Meadows & Meadows 1991; Jones *et al.* 1994; Whitford & Kay 1999). By creating holes or depressions that trap nutrients, seeds and water, burrowing vertebrates profoundly influence the physical and chemical properties of soils, and the germination and survival of plant seedlings. For example, in Australia, burrows created by Gould's sand goanna influence water infiltration rates and the distribution of mulga (*Acacia aneura*) woodlands (Whitford 1998), while pits excavated by kangaroos influence soil chemistry and the spatial heterogeneity of nutrient-rich sites in arid and semi-arid woodlands (Eldridge & Rath 2002).

To date, most Australian studies on vertebrate biopedturbators have focused on their effects on soil biology (Garkaklis *et al.* 1998, 2003; Whitford 1998; Eldridge & Rath 2002) or seedling germination and survival (Ashton & Bassett 1997; Theimer & Gehring 1999). By contrast, the effect of vertebrate biopedturbation on the behaviour of sympatric native animals has not been studied in detail. Many species respond to animals that create disturbance (especially humans) as potential predators (Frid & Dill 2002), and modify their behaviour to minimize the risk of predation (Lima 1998; Gill *et al.* 2001). For example, timber rattlesnakes *Crotalus horridus* abandon their preferred habitats (rocks) after capture or after the rocks are disturbed by humans (Brown 1993). Other studies on mammals and birds have found that human disturbance can cause habitat shifts (Boyle & Samson 1985), disruption of foraging activities (Gander & Ingold 1997), home range displacement (McLellan & Shackleton 1988) or reduced reproductive success (Giese 1996). Although the effects of human distur-

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bance on wildlife are well documented, native vertebrate species that disturb resources used by other organisms can also influence the evolution of behaviour, habitat selection and life histories of sympatric taxa (Lytle 2001). Theoretically, animals should avoid disturbed habitats, provided that the net benefits of shifting habitats outweighs the costs of remaining at disturbed sites (Gill *et al.* 2001). Although the predictions of the disturbance-risk theory are intuitive, few studies have investigated how biotic disturbance caused by native animals influences habitat selection by sympatric species.

In temperate forests of eastern Australia, the superb lyrebird *Menura novaehollandiae* creates local disturbances by constructing display mounds and more widespread disturbances by foraging for litter invertebrates. Lyrebirds use their powerful, clawed feet to rake leaf litter, and they displace large quantities of leaf litter and soil while foraging (Reilly 1988). For example, in bare areas of forest floor in Victorian *Eucalyptus regnans* forests, lyrebirds displace up to 200 tonnes of soil per hectare annually (Ashton & Bassett 1997). In other forests, lyrebirds turn over the entire forest floor within 20–31 months (Adamson *et al.* 1983; Ashton & Bassett 1997). By turning leaf litter and raking soil, lyrebirds dramatically influence plant community structure (Ellis 1971; Ashton & Bassett 1997). Foraging lyrebirds also displace rocks weighing up to 2 kg and eat invertebrates that live under these shelter sites (Adamson *et al.* 1983; Ashton & Bassett 1997). Adamson *et al.* (1983) reported that lyrebirds preferred to feed around and under rocks, and substantially enlarged the areal extent of exposed rock outcrop during their foraging activities.

To date, the impact of lyrebird disturbance on animals that shelter underneath sandstone rocks has not been studied. Rock outcrops support distinct biotic assemblages, including many endemic taxa, but they are fragile ecosystems that are particularly vulnerable to disturbance (Shine *et al.* 1998; Porembski & Barthlott 2000; Webb *et al.* 2002a). In the Sydney region of eastern Australia, sandstone rock outcrops contain a high diversity of vertebrates and invertebrates with high conservation significance (Recher *et al.* 1993; Cogger 2000; Goldsbrough *et al.* 2003). In Morton National Park, two species of nocturnal snakes, the endangered broad-headed snake *Hoplocephalus bungaroides* and the common small-eyed snake *Cryptophis nigrescens,* use sandstone rocks as diurnal thermoregulatory sites from April to November (Webb & Shine 1998a; Webb *et al.* 2003, 2004). Because juveniles of both of these snakes shelter under small stones, lyrebirds might disturb snake retreat sites, and may attack small snakes (Webb & Whiting 2005). If lyrebird rock disturbance occurs frequently, we predict that juvenile snakes should avoid high-risk habitats, and use safer habitats as diurnal thermoregulatory sites.

Here we investigate whether the superb lyrebird disturbs sandstone rocks that juvenile *H. bungaroides* and *C. nigrescens* use as diurnal shelter sites. We address five questions: (i) Do lyrebirds displace rocks used by snakes? (ii) Do they attack snakes sheltering underneath rocks? (iii) Do lyrebirds disturb rocks on soil and rock substrates? (iv) Which rocks confer the greatest thermal benefits to snakes? and (v) Do snakes avoid retreat sites disturbed by lyrebirds? To answer these questions, we placed 900 plasticine snake replicas underneath rocks lying on rock and soil substrates and quantified disturbance to rocks and predation on snake models over a 6-week period. To determine whether lyrebird disturbance varied across the landscape, we replicated our study on three geographically isolated sandstone plateaux. To estimate the thermal benefits conferred by rocks on rock and soil substrates, we quantified the thermal environments in these two microhabitats and estimated the abundance of the two types of retreat site. To quantify habitat selection by juvenile snakes, we used data from a 10-year (1992–2002) mark–recapture study, and compared the physical characteristics of rocks used by snakes to those disturbed by lyrebirds.

MATERIALS AND METHODS

Study species

The study species are small (<90 cm total length), viviparous nocturnal snakes from the family Elapidae. The endangered broad-headed snake *H. bungaroides* is a habitat specialist that is restricted to sandstone habitats within a 200-km radius of the city of Sydney, NSW, Australia. The small-eyed snake *C. nigrescens* is a habitat generalist with a broad geographical range in eastern Australia, from southern Victoria to northern Queensland (Cogger 2000). In Morton National Park, these snakes shelter under small stones adjacent to cliffs during the cooler months (March–November). Individuals of both snake species rarely bask, but spend long-time periods sheltering underneath individual rocks (up to 4 weeks), and some individuals return to the same rocks each year (Webb & Shine 1998a). The populations examined here have been the subject of long-term radiotelemetry and mark–recapture studies, and their ecology and life history are described in detail elsewhere (Webb *et al.* 2002b, 2003).

Snake models

We used plasticine snake replicas to estimate the frequency of lyrebird predation on snakes sheltering under stones on rock and soil substrates. We made snake replicas from black plasticine (Rainbow modelling clay, Newbound Pty Ltd, Rydalmere, NSW, Australia). The plasticine was prepackaged in 500-g blocks, separated into individual pieces (diameter 5 mm), closely approximating the body diameter of a juvenile snake. We made all models 275 mm long, the average total length of a hatchling broad-headed snake or juvenile small-eyed snake (Webb *et al.* 2003). For each model, we smoothed out any inconsistencies in the plasticine, expanded one end to resemble a snake's head, and modified the opposite end to resemble a tail.

Estimating lyrebird rock disturbance and predation

To investigate whether biotic disturbance varied across the landscape, we selected three geographically isolated plateaux (DG, MG and YL, each approximately 2.5 km apart) where *H. bungaroides* and *C. nigrescens* occur. At each plateau, we selected three sites (all >450 m apart) to ensure adequate spatial replication. On each site, we walked a 500-m transect parallel to the cliffs, keeping within 50 m of the cliffs to ensure that models were placed in habitats used by *H. bungaroides* and *C. nigrescens* (open areas of outcropping rock near cliffs). Thus, experimental transects were not straight, but deviated depending on the local topography of the site. On each transect we drew straws to determine the placement of the first model (underneath a stone lying on rock *vs.* on soil), and thereafter we randomly selected models from a box and placed them at 5-m intervals in alternate sequence. We placed 100 models on each transect, 50 hidden beneath stones lying flush on bare rock substrates and 50 under small rocks lying flush on soil substrates. We positioned all models in an identical S-shape and firmly pressed them onto the substrate before covering them with a randomly chosen rock. All rocks had flat surfaces and were large enough to conceal a small snake (mean length = 168 mm, range 85–280 mm). We numbered the underside of each rock with a white paint pen so that we could determine whether the rocks had been flipped over. We placed 900 models in the field in April 2003, and removed them after 6 weeks. At the end of the experiment, we measured the linear dimensions (length, diameter, thickness, to nearest mm) of all rocks that we could locate ($n = 855$), and the mass of disturbed rocks ($n = 113$) and a random sample of undisturbed rocks ($n = 122$).

Scoring predation on plasticine replicas

We filmed each model with predation marks with a digital video camera in the field, and retained a subset of models with identical imprints for later comparison with marks made by known predators. We also scored the location of predation imprints according to snake body region: head, mid-body and tail. We used published data for the study area (Fox 1988) to determine which mammalian predators co-occur with snakes, and we compared the predation marks on plasticine replicas with the imprints made by the teeth of these species.

Thermal environment underneath rocks

Previous studies have shown that exposed, thin rocks on rock substrates allow nocturnal snakes to achieve 'preferred' body temperatures during part of the day (Webb & Shine 1998a). To assess whether rocks lying on soil also provide snakes with thermally suitable retreat sites, we measured temperatures under rocks lying on soil and rock substrates on an exposed 5 m × 5 m quadrat on the YL plateau. We selected 10 pairs of rocks (each pair with similar dimensions) that spanned a wide range of sizes and thicknesses (mean length = 256 mm, range 138–450 mm long, mean thickness = 57 mm, range 18–130 mm), glued a miniature data logger (Thermochron iButton, Dallas Semiconductor, Dallas, TX, USA) to the middle underside of each rock, and placed one rock from each pair on bare soil and the other on bare rock. Temperatures were measured every 15 min from 9 to 29 May 2003. To assess the suitability of rocks for snake thermoregulation, we calculated the time period each day that rock temperatures fell within the snake's set-point range (28.1–31.1°C, Webb & Shine 1998a,b).

Retreat site selection by snakes

We used data from a long-term (1992–2002) mark–recapture study of *C. nigrescens* and *H. bungaroides* to determine whether snakes were using retreat sites non-randomly with respect to rock size and substrate. The mark–recapture study was carried out at three study sites on the YL plateau, and full details of the locations of sites, dates of field trips and general methods are provided elsewhere (Webb *et al.* 2002a, 2003). During the study all snakes encountered under rocks were permanently marked with miniature PIT tags and their size, sex and reproductive status, recorded. For each snake rock, we recorded the physical dimensions (length, width, thickness), substrate (rock or soil), and visually assessed the percentage canopy cover above the rock. We numbered each rock (with a paint pen, underneath) and recorded its exact location with a Global Positioning System (GPS, (Garmin GPS 12XL, Garmin International, Olathe, KS, USA)). We also recorded these physical characteristics for the first four random rocks encountered on the four compass directions (N, S, E, W) within 5 m of the snake's rock. To determine whether lyrebirds disturb rocks that snakes could potentially use as retreat sites, we compared the physical attributes (length, width, thickness and substrate) of 66 rocks used by juvenile snakes (SVLs < 300 mm, similar in size to the plasticine models) to disturbed rocks. To assess whether snakes were using rocks non-randomly, we compared 'snake' rocks with a random sample of 264 available rocks not used by snakes.

Statistical analysis

We used logistic regression to investigate whether rock disturbance (disturbed *vs.* not disturbed) was explained by rock size, substrate, or plateau. To avoid problems associated with collinearity among predictors (Hosmer & Lemeshow 1989), we included a single measure of rock size (rock size = length × width × thickness) in the models. We used rock size in our analyses because it was significantly correlated with rock mass ($r^2 = 0.77$, $n = 225$ rocks, $P < 0.0001$), and thus, provides a reasonable estimate of the force required to dislodge a rock. Because lyrebirds rarely displace rocks >2 kg in mass (Adamson *et al.* 1983), we hypothesized that rock size would influence the probability of rock disturbance in this system. After identifying the factors that explained the likelihood of rock disturbance, we compared the size of disturbed *versus* non-disturbed rocks using analysis of variance. Prior to statistical analyses, we checked data for non-normality and heterogeneous variances, and log-transformed mass data, arc-sin transformed proportional data, and square-root transformed rock size data (Underwood 1997).

RESULTS

Spatial variation in rock size

Although we placed rocks with similar lengths on our experimental transects (Table 1), rocks from different plateaux varied in their thickness and size (Table 2). *Post hoc* tests (Fisher's least significant difference (LSD)) showed that rocks from the DG plateau were significantly thicker than rocks from the other two plateaux (DG > MG = YL, Table 1). Rocks from the DG and MG plateaux were also larger (and therefore, heavier) than rocks from the YL plateau (DG = MG > YL, Table 1). On all plateaux, rocks on rock substrates were larger than rocks on soil substrates (Table 2, means of 786.4 *vs.* 681.5 cm^3, respectively, for raw data).

Frequency of disturbance to rocks

Animals disturbed 113 of 900 experimental rocks (12.6%) during the 6-week study, either by flipping them over (77 rocks) or by displacing them horizontally (36 rocks). Identification of imprints on the plasticine replicas (see below) and scratch marks adjacent to disturbed rocks suggested that lyrebirds were the major agents of rock disturbance (56.7%), followed by unidentified predators (27.4%), unidentified mammals (8.8%), wallabies (4.4%) and wombats (2.7%). The frequency of rock disturbance was similar on

Table 1. Results of two factor nested analyses of variance for the effects of substrate and spatial scale on rock thickness (raw data) and size (square-root transformed). Significant P-values are shown in bold font

Source	d.f.	MS	*F*	*P*
Rock thickness				
Substrate	1	182.76	1.01	0.32
Plateau	2	2557.58	14.11	**<0.0001**
Substrate × plateau	2	105.95	0.58	0.56
Transect (plateau)	6	465.03	2.57	**0.02**
Error	843	181.28		
Rock size				
Substrate	1	613.81	11.84	**0.001**
Plateau	2	288.53	5.66	**0.004**
Substrate × plateau	2	30.95	0.60	0.55
Transect (plateau)	6	74.78	1.44	0.20
Error	843	51.85		

Plateau and substrate were fixed factors, and transect (random factor) was nested within plateau.

Table 2. Physical dimensions of natural rocks that were placed on nine 500-m-long transects on three sandstone plateaux to provide an estimate of the rate of lyrebird disturbance to rocks during a 6-week period

Plateau	Sample size	Rock length (cm)	Rock diameter (cm)	Rock thickness (mm)	Rock size (cm^3)
DG	263	16.4 (3.3)	11.7 (2.5)	39.1 (16.3)	791.4 (450.7)
MG	296	17.1 (3.5)	11.7 (2.4)	35.6 (11.9)	748.0 (392.3)
YL	296	16.9 (3.3)	11.6 (2.5)	33.2 (12.3)	675.1 (368.5)

Table shows mean values for raw data with standard deviations in parentheses. Although 100 rocks were placed on each transect (300 rocks on each plateau), the final sample sizes differ among plateaux because we could not locate all rocks on transects at the end of the study.

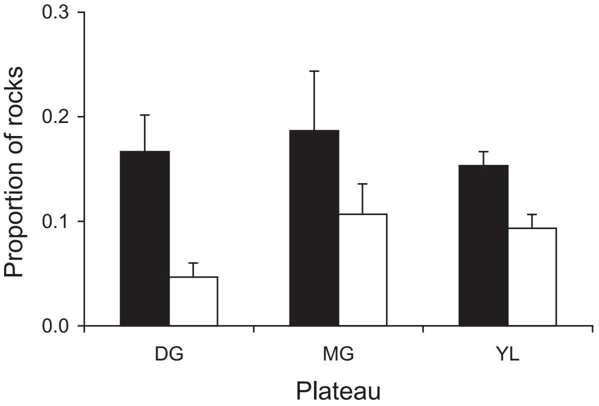

Fig. 1. Frequency of biotic disturbance to small sandstone rocks on (■) soil and (□) rock substrates on three sandstone plateaux in Morton National Park, NSW, Australia. Rocks on soil were disturbed twice as frequently as rocks on rock during the 6-week study.

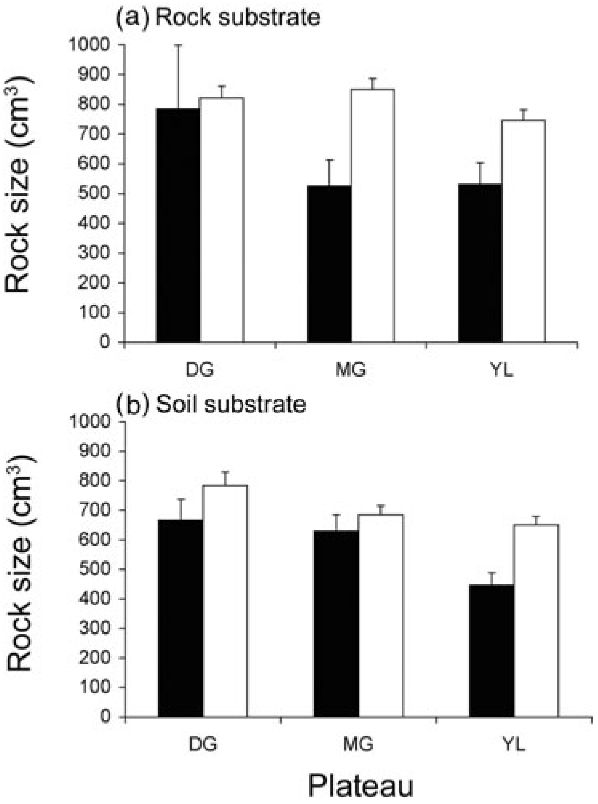

Fig. 2. Mean size of (■) disturbed *versus* (□) undisturbed rocks after a 6-week period. Rocks disturbed by animals were larger than undisturbed rocks on both (a) rock and (b) soil substrates on the three study plateaux. Error bars denote standard errors.

the three plateaux (two-factor ANOVA, $F_{2,12} = 0.83$, $P = 0.46$), but rocks lying on soil substrates were disturbed more frequently than rocks on rock substrates (16.9% *vs.* 8.2%; $F_{1,12} = 11.52$, $P = 0.005$, interaction $F_{2,12} = 0.48$, $P = 0.63$, Fig. 1).

Effects of substrate and rock size on disturbance

We used logistic regression to analyse the determinants of rock disturbance, with plateau, substrate and rock size as the independent variables, and whether a rock was undisturbed or disturbed as the dependent variable. Because rock size varied between plateaux and among substrates (Table 2), we included interactions between the independent variables in the model. This analysis showed that substrate and rock size were highly significant; log-likelihood ratio tests yielded Chi-square values of 14.14 for substrate (d.f. = 1, $P = 0.0007$) and 19.51 for rock size (d.f. = 1, $P < 0.0001$). None of the other factors, or interactions between factors, were significant in the model. In other words, the likelihood that a rock would be disturbed depended on its size and substrate. Rocks disturbed by animals were smaller than undisturbed rocks, and this pattern was similar across plateaux (two-factor ANOVA, disturbance $F_{1,849} = 20.95$, $P < 0.0001$, plateau $F_{2,849} = 4.61$, $P = 0.01$, plateau × disturbance $F_{2,849} = 0.73$, $P = 0.48$), and between substrates (disturbance $F_{1,849} = 19.74$, $P < 0.0001$, substrate $F_{2,849} = 0.52$, $P = 0.47$, substrate × disturbance $F_{2,849} = 2.31$, $P = 0.13$, Fig. 2).

We used logistic regression to examine whether the nature of biotic disturbance to rocks (i.e. whether a rock was flipped over *vs.* displaced horizontally) was influenced by substrate, rock mass or an interaction between the two factors. This analysis showed that rock mass and the interaction between mass and substrate were significant; log-likelihood ratio tests yielded Chi-square values of 5.06 for mass (d.f. = 1, $P = 0.03$) and 4.15 for mass × substrate (d.f. = 1, $P = 0.04$). Displaced rocks were significantly heavier than flipped rocks on rock substrates, but not on soil substrates (substrate, $F_{1,109} = 0.09$, $P = 0.77$, disturbance $F_{1,109} = 7.01$, $P = 0.01$, interaction $F_{1,109} = 6.72$, $P = 0.01$, see Fig. 3). This pattern persisted even when we restricted the analysis to rocks disturbed by lyrebirds (substrate, $F_{1,60} = 0.09$, $P = 0.77$, disturbance $F_{1,60} = 5.48$, $P = 0.02$, interaction $F_{1,60} = 6.24$, $P = 0.02$). In other words, the ability of lyrebirds to turn over rocks (presumably, with their beaks and talons) was influenced by the substrate below; the birds could not flip over heavy rocks on rock substrates, but they could do so on soil substrates.

Predation on models under disturbed rocks

Predators attacked 49.6% of the plasticine snake models under disturbed rocks. Of 56 predatory attacks on plasticine snake models, lyrebirds attacked 39 models and mammals attacked 11. Lyrebird attacks on the plasticine replicas were easily identifiable by the presence of a pair of V-shaped marks on opposite sides of the replica (Fig. 4a,b). The uniform size and shape of the beak marks on the replicas, and the presence of extensive lyrebird scratch marks beside disturbed rocks, suggests that the lyrebird was responsible for avian attacks on plasticine models. Most birds attacked the head (63% of models) or tail region (29.3% of models) of the replicas, and these two regions contained 50.0% and 35.2% of all beak marks, respectively. In several cases the birds had torn the replicas in two or had displaced them several metres. Of models attacked by lyrebirds, 26 were under stones that had been flipped over (19 on soil, seven on rock) and 13 were under rocks that had been displaced sideways (five on soil, eight on rock). Six models could not be located, but lyrebird scratch marks beside disturbed rocks suggested that lyrebirds had displaced five of these models.

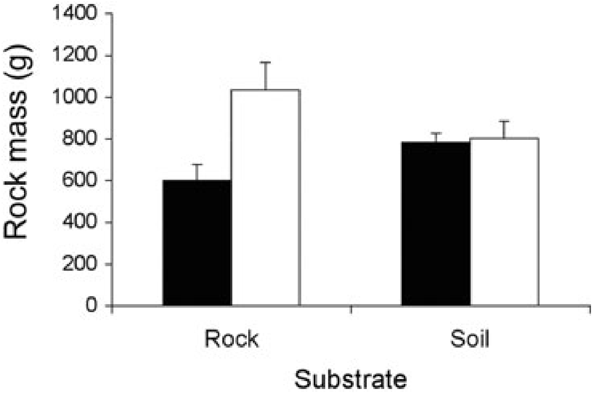

Fig. 3. The type of physical disturbance to a rock depended on its mass and the substrate it was lying on. Rocks displaced by animals (□) were heavier than flipped rocks (■) on rock substrates, but not on soil substrates.

Mammal predation on plasticine models was characterized by the presence of a pair of incisor marks on the dorsal surface (Fig. 4c,d) or by the presence of multiple tooth marks (Fig. 4e). Based on comparison of tooth marks with a reference collection of mammalian skulls, the mammal species responsible for most attacks were the bush rat *Rattus fuscipes* (Fig. 4c) and the sandstone antechinus *Antechinus agilis* (Fig. 4e). Several larger unidentified bite marks were recorded on two replicas (Fig. 4f). Although they probably did not flip the rocks, wombats had squashed the snake replicas beside three flipped stones. Of 48 plasticine snake replicas that were not attacked by predators, 21 were stuck to the bottom of the rocks (five displaced rocks, 16 flipped rocks) and 27 had no obvious predatory marks on them, even though the rocks had been displaced (10 on soil) or flipped (12 on soil, five on rock).

Thermal environment under rocks on soil and rock substrates

The substrate beneath a rock significantly influenced its thermal regime and, therefore, the ability of snakes to maintain preferred body temperatures. Rocks on soil substrates provided snakes with set-point temperatures for longer-time periods per day, and on more days, than did rocks on rock substrates (means of 52.0 min *vs.* 24.9 min, $F_{1,18} = 4.98$, $P = 0.04$; means

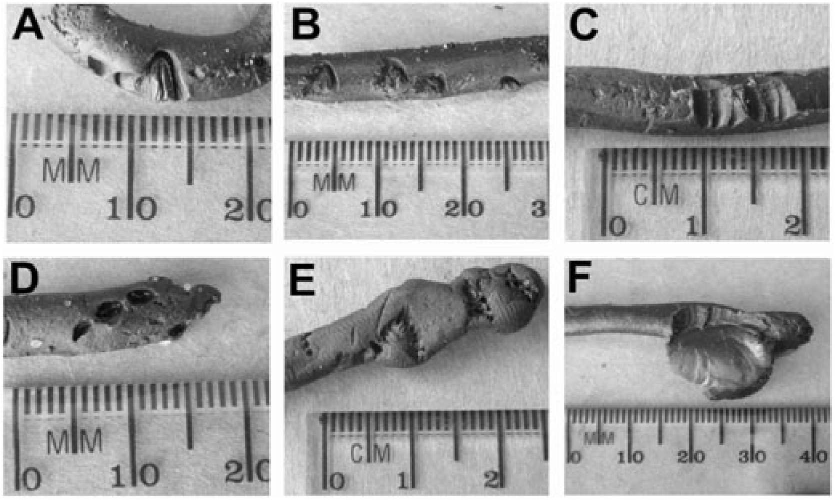

Fig. 4. Imprints left by predatory attacks on plasticine snake models in the field. Figure shows (A) V-shaped beak mark from a superb lyrebird; (B) multiple lyrebird beak marks on the same model; (C) incisor marks from a large rodent (probably the native bush rat *Rattus fuscipes*); (D) tooth marks from an unidentified mammal; (E) tooth marks from the dasyurid marsupial *Antechinus agilis*; (F) palate imprint from an unknown mammal.

of 5.5 days *vs.* 2.8 days, $F_{1,18} = 4.26$, $P = 0.05$). Rock thickness was a good predictor of the number of days that snakes could achieve preferred body temperatures for rocks on soil substrates ($r^2 = 0.66$, $P = 0.004$), but not for rocks on rock substrates ($r^2 = 0.06$, $P = 0.49$). In other words, thinner rocks were better for snake thermoregulation on soil substrates, whereas both thin and thick rocks (18–130 mm thick in our sample) on rock substrates were equally suitable for snake thermoregulation. Because rock thickness increased with rock diameter ($r^2 = 0.40$, $P < 0.0001$, $n = 264$), smaller rocks on soil were better for snake thermoregulation than were larger rocks, whereas both large and small rocks were suitable for snake thermoregulation on rock substrates.

Habitat selection by snakes in disturbed habitats

During the 10-year mark–recapture study we captured 75 juvenile snakes (44 *H. bungaroides* and 31 *C. nigrescens*) under 66 individual rocks. Nine rocks were used as retreat sites by both species of snake (at different times), but we never observed both snake species sharing the same rock at the same time. Overall, rocks used by snakes were significantly larger than rocks disturbed by animals ($F_{1,176} = 227.3$, $P < 0.0001$). Thus, although 24% of snake rocks were <30 cm long and could potentially be disturbed by superb lyrebirds, most snakes used rocks that were too heavy for lyrebirds to disturb (Fig. 5a). Did the snakes select rocks non-randomly? To answer this question, we assigned shared rocks to either *C. nigrescens* or *H. bungaroides*, and compared the length, thickness and substrate of the three rock categories: *R. nigrescens*, *H. bungaroides* and available rocks. The mean sizes of rocks used by both snake species were very similar to available rocks (rock length: $F_{2,327} = 0.44$, $P = 0.64$, rock diameter: $F_{2,327} = 0.47$, $P = 0.62$). However, both snake species selected rocks that were significantly thinner than available rocks ($F_{2,327} = 11.22$, $P < 0.0001$, Fisher's LSD *post hoc* tests, Available > *H. bungaroides* = *R. nigrescens*). More importantly, both species of snake avoided rocks on soil substrates ($\chi^2 = 23.87$, $P < 0.0001$, with correction for small sample size), even though rocks on soil substrates comprised 46.2% of available rocks on the study sites (Fig. 5b). Indeed, only five snakes (three *H. bungaroides* and two *C. nigrescens*) used rocks on soil substrates during the 10-year study.

DISCUSSION

During the 6-week study animals disturbed 12.6% of our experimental rocks. Biotic disturbance to rocks was widespread and occurred on the three plateaux that we sampled. Superb lyrebirds were the major agents of disturbance, and they disturbed 7.1% of small rocks on transects near the western cliffs. A previous study reported that lyrebirds forage mainly on east and south facing slopes (Adamson *et al.* 1983), but our results show that lyrebirds also forage on the plateau tops. Our most interesting finding was that lyrebirds disturbed small stones on bare rock outcrops, a critical habitat for the endangered broad-headed snake. Although lyrebirds forage by scratching leaf litter, 69% of the rocks they disturbed had been flipped over rather than raked sideways. The fact that lyrebirds overturned rocks in areas devoid of leaf litter suggests that they were searching for prey underneath these stones. Indeed, 39.5% of the plasticine snake models hidden under disturbed rocks had beak imprints consistent with lyrebird attacks (see Fig. 4a). Although a previous dietary study concluded that lyrebirds were insectivorous (Lill 1996), our results sug-

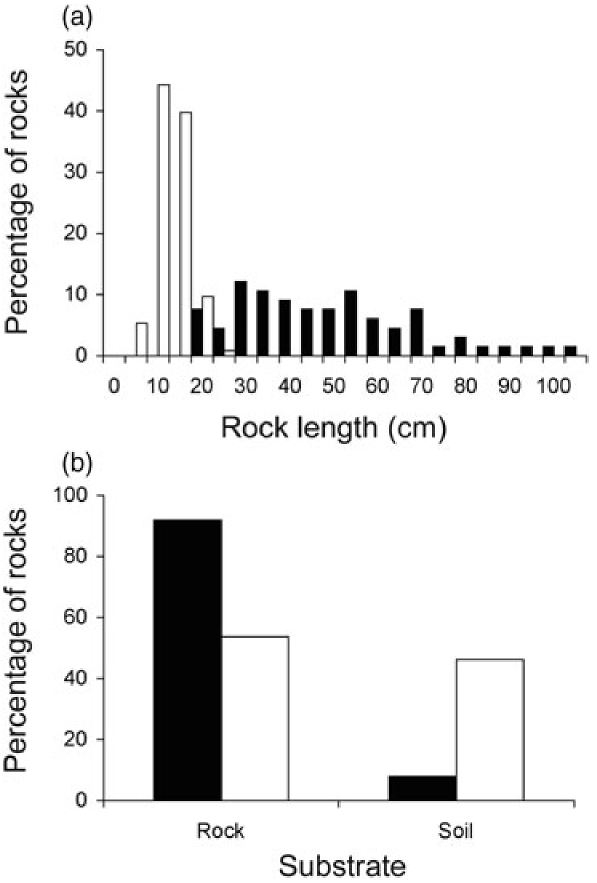

Fig. 5. Size distributions of rocks disturbed by animals on transects *versus* those used by juvenile snakes (*Cryptophis nigrescens* and *Hoplocephalus bungaroides*) over a 10-year period (1992–2002) on the YL plateau, Morton National Park, NSW. Juveniles of both snake species showed similar patterns of habitat selection, and (■) used rocks that were (a) larger than those (□) disturbed by animals, and (b) avoided rocks on soil substrates.

gest that lyrebirds living in rocky habitats may also feed on small ectothermic vertebrates (snakes and lizards) that shelter under stones.

One caveat of our experiment is that we estimated the frequency of lyrebird predation on snakes by using plasticine models that lack movement. Clearly, if lyrebirds use prey movement to orientate feeding strikes, then we would have underestimated the true frequency of lyrebird predation on live snakes. A second problem was that some of the plasticine models were stuck to the surface of the overlying rock, and hence, would not be visible to predators once the rocks were overturned. Again, this would have meant that we underestimated predation rates on snakes. Despite these problems, our data do show that lyrebirds will attack snake-like objects under stones. The fact that 85.2% of all beak marks were directed to the head and tail regions of the models suggests that lyrebirds treated the replicas as if they were live snakes (Smith 1973; Brodie 1993). Because lyrebirds forage most intensively early in the morning (Reilly 1988), when snakes sheltering under rocks have low body temperatures and impaired locomotor performance (Webb & Shine 1998b; Llewelyn *et al.* 2005), the birds would probably have little difficulty capturing slow-moving snakes.

Our results suggest that lyrebird rock disturbance will have important consequences for rock-dwelling snakes. First, because lyrebirds probably attack live snakes, the costs of choosing a poor retreat site (i.e. with high probability of disturbance) will be high in this system. According to the predation risk hypothesis, snakes should avoid high-risk habitats (Lima & Dill 1990), provided that the disturbance occurs frequently within an animal's lifetime (Lytle 2001), and safer thermoregulatory sites are available. Because juvenile broad-headed snakes and small-eyed snakes shelter under rocks during 8 months of the year (April to November) when lyrebirds forage intensively (Reilly 1988), both species of snake are likely to encounter lyrebird disturbance.

Do snakes avoid high-risk habitats as predicted by the predation risk hypothesis? On our study plateaux, lyrebirds disturbed rocks on soil substrates twice as frequently as rocks on rock substrates, and disturbed small rocks (mean mass = 0.75 kg, range 0.2–2.1 kg) rather than large rocks. Thus, snakes could minimize predation risk by choosing rocks on rock substrates or large rocks too big for animals to disturb. However, because they do not bask, the snakes must balance the benefits of thermoregulation against the risk of predation when selecting retreat sites (Huey & Slatkin 1976; Huey *et al.* 1989; Lima & Dill 1990). Intriguingly, small rocks on soil substrates allowed snakes to achieve set-point temperatures for significantly longer-time periods than did rocks on rock substrates. Although rocks on soil were abundant on the YL plateau, only two *C. nigrescens* and three *H. bungaroides* used rocks on soil substrates during the 10-year mark–recapture study. Thus, both species of nocturnal snake may have responded to disturbance by avoiding rocks on soil, and by selecting larger rocks that are less likely to be displaced by animals (see Fig. 5).

Although our results are consistent with the predation risk hypothesis, alternative explanations are possible. First, the broad-headed snake's use of rocks on rock substrates may be related to its ambush foraging strategy and diet that includes a rock-dwelling gecko (*Oedura lesueurii*) that also avoids rocks on soil (Schlesinger & Shine 1994). In contrast, the small-eyed snake is a habitat generalist that is often found under cover objects (bark, logs, rocks) lying on soil substrates (Cogger 2000). Why this species avoids rocks on soil at our study sites is less clear; possibly, the snakes may be unable to burrow under rocks lying on soil substrates. Finally, both snake species may prefer to use large rocks as retreat sites because larger rocks provide more thermally heterogeneous environments than do smaller rocks (Kearney 2002), and so may allow snakes to thermoregulate more precisely. Nonetheless, the high incidence of lyrebird (and *A. agilis*) attacks on snake models under small stones suggests that predation risk also influences habitat selection by snakes in this system (Webb & Whiting in press).

We hypothesize that lyrebird disturbance has three important effects on rock-dwelling vertebrate and invertebrate communities. First, by disturbing rocks and eating animals that live underneath them, lyrebirds could increase invertebrate species richness by removing dominant competitors or predators (e.g. lizards, spiders and ants, Goldsbrough *et al.* 2003) from rocks (Huston 1994). This hypothesis could be tested by carrying out long-term lyrebird field-exclosure experiments, and by removing dominant predators from outcrops. Second, on larger spatial scales, lyrebirds may influence the distribution of disturbance-sensitive species. Because lyrebirds forage most intensively on slopes and gullies (Adamson *et al.* 1983), rates of rock disturbance in these areas are likely to be much higher than on plateau tops. Less disturbed sites, such as ridge tops, or areas where lyrebirds are absent, may therefore serve as refuges for sensitive species. Third, by disturbing small stones and rendering such sites unsuitable for colonization by long-lived species, lyrebird disturbance could influence competitive interactions among rock-dwelling taxa. For example, *H. bungaroides* and *C. nigrescens* both select similar-sized rocks (Fig. 5), but heterospecifics do not share rocks, nor do males share rocks with conspecific males (Webb *et al.* 2004). Thus, on outcrops where rocks are a limiting resource, disturbance may intensify competitive interactions between these two snake species. Moreover, because *C. nigrescens* occasionally eats other snakes (Shine 1984), and grows faster than *H. bungaroides* (Webb *et al*. 2003), large male *C. nigrescens* could potentially exclude juvenile *H. bungaroides* from hot rocks, thereby preventing the endangered species from colonizing disturbed sites. We predict that intense competitive interactions will occur on densely vegetated eastern facing cliffs, where canopy gaps and 'hot' rocks are rare (Pringle *et al*. 2003), and where lyrebird disturbance is high (Adamson *et al*. 1983).

In conclusion, our results show that superb lyrebirds are important agents of disturbance on sandstone rock outcrops in south-east Australia. The frequency and spatial extent of lyrebird disturbance – two factors likely to influence biodiversity in these systems (Huston 1994; Wootton 1998) – is likely to vary temporally in response to changes in vegetation structure and the intensity and frequency of fire (Adamson *et al*. 1983). Lyrebird densities are highest in late successional forests where fire is infrequent (e.g. Morton National Park), and lowest in open grassland or heath communities where fire is more frequent (Reilly 1988; Smith 1988). Consequently, we predict that lyrebird disturbance to rock outcrops will be rare in open heath communities and more frequent in closed forests. Because high-intensity fires can decrease lyrebird abundance (Adamson *et al*. 1983), the frequency, intensity and spatial extent of fires will directly influence the frequency and magnitude of biotic disturbance to sandstone outcrops. Currently, the effects of fire and European fire suppression activities on the fauna inhabiting sandstone rock outcrops in eastern Australia are poorly understood (Whelan 2002). Future experimental studies to investigate how fire and biotic disturbance influence the biota of sandstone rock outcrops would greatly improve our understanding of these important and understudied ecosystems.

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