ANNUAL SURVIVAL RATES OF BOWER-OWNING MALE GREAT BOWERBIRDS *Ptilonorhynchus nuchalis* IN TOWNSVILLE, QUEENSLAND

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This study documents the annual survival rate of bower-owning male Great Bowerbirds *Ptilonorhynchus nuchalis* in Townsville, Queensland. The mean survival rate of bower-owning males was 84 per cent from 2003 to 2007. The estimate of survival is slightly lower than that recorded for bower-owning males of three other species (range: 90 – 93%). Lower estimates could be a consequence of dispersion from the study area, particularly of younger birds. Lower estimates could also have occurred because Townsville is a suburban environment containing hazards that bowerbirds do not experience under natural conditions. Over the course of the study, one male drowned in a swimming pool and one appeared to have died due to predation. At least eight unbanded individuals (sex and status unknown) were struck by vehicles on the study site.

INTRODUCTION

Males of most bowerbird species (Ptilonorhynchidae) are promiscuous and build bowers to attract females with whom they mate. Several studies have shown that bowerbirds exhibit high annual survival rates. Though data for females are limited, the survival rates for bower-owning males of three species ranged from 90 to 93 per cent (reviewed in Frith and Frith 2004). However, additional studies are needed to determine whether high survival rates are a family-wide trend in the Ptilonorhynchidae.

Great Bowerbirds *Ptilonorhynchus nuchalis* live throughout northern Australia and build one of the largest and most well-decorated bowers of the Australian bowerbird species. Structures can exceed one metre in length and are often decorated with more than 1,000 objects, including rocks, bones, shells, leaves and fruit (Frith and Frith 2004). Great Bowerbirds are also one of the few bowerbird species that have successfully adapted to human development. In Townsville, males frequently build bowers in populated areas, such as parks, school grounds and private residences (Frith *et al.* 1996; Doerr 2008); however, this close association with humans could affect their survival.

No studies to date have documented survival rates in any population of this species. This study reports the annual survival rates of bower-owning male Great Bowerbirds in Townsville from 2003 to 2007.

METHODS

In 2000, researchers at James Cook University began banding Great Bowerbirds in Townsville, Queensland (19°19'S, 146°46'E), and I banded and monitored bower-owning males in Townsville from 2003 to 2007. Birds were banded at three adjacent areas encompassing 15 square kilometres: the James Cook University campus, the Lavarack Barracks military base, and the suburb of Annandale. Roads, such as the Bruce Highway, intersected all three study areas. Males built their bowers underneath bushes, and many bowers were adjacent to

areas used by pedestrians, such as footpaths and car parks. Males were captured at their bowers using mistnets or spring-loaded mammal traps baited with fresh fruit and bower decorations. A metal band issued from the Australian Bird and Bat Banding Scheme, as well as a unique combination of three colour bands were placed on each male's leg. One colour band was placed above the metal band, and the other two were placed on the opposite leg.

Once a male was banded, I returned to the bower on a regular basis to determine whether the banded individual was the owner. At some bowers, I monitored males using a motion-activated camcorder system, which recorded all activity at bowers for the majority of the breeding season (September through mid-December). At other bowers, I conducted one- to four-hour observation sessions at least twice each breeding season to determine the identity of the bower owner. In addition, I visited most bowers every 10 to 14 days to count bower decorations, and I noted the identity of individuals present during those times. Following Madden *et al.* (2004), I defined bower owners as males that were present more than 75 per cent of the time for which I recorded at least one bird present. All presumed bower owners regularly maintained and displayed at their bowers.

Male bowerbirds exhibit high fidelity to their bower sites (Frith and Frith 2004), and male Great Bowerbirds in Townsville typically build new bowers within 33 ± 43 metres (mean ± *sd*; range: 1–127 m) of the bowers they built the previous breeding season (Doerr 2008). Therefore, I observed whether male bower-owners returned to their bower sites in successive years, and I assumed that the bower owner had died if I could not relocate the male or his bower anywhere on the study site, or on lands immediately adjacent to the study site, during the following breeding season. Previous studies of survivorship in bowerbirds have made the same assumption (Borgia 1993). Because new bowers were built over the course of the study while a few established bowers were abandoned, the number of males that I monitored differs slightly between years.

To calculate survival rates for each year, I used the equation:

$$S_i = 100 \ (b_i \ / \ a_{i-1})$$

where: S_i represents survival to year *i; a* is the number of banded birds present in year *i-1*; and *b* is the number present the following breeding season. I performed this calculation separately for each pair of study years (2003 to 2004, 2004 to 2005, etc.). To calculate a single value for the mean annual survival rate over the four years of the study, I used the equation:

$$S = 100 \ (\textstyle\sum_{i=1}^{x} b_{i+1} \ / \ \sum_{i=1}^{x} a_i) \tag{1}$$

where: *a* is the number of banded birds present in year *i*; *b* is the number still present the following breeding season; and *x* is the number of study years (Nicholls and Woinarski 1988). This equation has been used to estimate survival rates of bower-owning male Tooth-billed Bowerbirds *Scenopoeetes dentirostris* (Frith and Frith 1995). Because males in their first year of bower ownership may be more likely to die or disperse from the study area than more established males (Borgia and Gore 1986; Frith and Frith 2004), I also used this equation to create separate survival estimates for males in their first year of bower ownership and males that had been bower owners for two or more years. A value for 'years of bower ownership' could not be assigned to nine males during the first year in which they were monitored because it was unknown whether these males had been at their bowers for one or more years; these data points were not included in the analysis of survival rates according to years of ownership. Finally, I performed a 2 x 4 Contingency Table analysis to determine whether survival rates differed between study years.

RESULTS

The mean annual survival rate over the four years of the study was 84 per cent (range: 74 – 93%; Table 1). Seven of the 13 males that were bower owners in 2000 were still owners in 2007 – a minimum of seven years of ownership. Survival rates did not differ significantly between study years (2 x 4 Contingency Table, $\chi^2 = 4.35$, df = 3, $P < 0.23$). Males that were in their first year of bower ownership had a survival rate of 61 per cent, while males that had been bower owners for two or more years had a survival rate of 89 per cent (Table 2).

On 19 September 2003, the staff at Lavarack Barracks found one bower-owning male dead in a swimming pool. This male was in his first year of bower ownership. A bower-owning male at James Cook University (years of bower ownership unknown) was probably predated: I observed the male at his bower on 14 September 2004; found a mass of bowerbird feathers at his bower the following morning; and never again saw the owner. Though I did not know the cause of death for any other bower owners, I found the bodies of at least eight bowerbirds along the side of the Bruce Highway, which intersects the study area. All individuals appeared to have been struck by vehicles. The skeletal remains of a banded, bower-owning male were found in a car park at Lavarack Barracks in March 2007 (C. Gould pers. comm.), but the cause of death was unknown. This male had owned a bower site for at least seven years.

DISCUSSION

Like other bowerbird species, bower-owning male Great Bowerbirds in Townsville exhibited high annual survivorship. The mean survival rate over the four years of the study was 84 per cent (*sd* = 0.034). In previous studies, survival rates of bower-owning males were 90 per cent in Tooth-billed Bowerbirds; 91 per cent in Golden Bowerbirds *Amblyornis newtoniana*; and 93 per cent in Satin Bowerbirds *Ptilonorhynchus violaceus* (Borgia 1993, reviewed in Frith and Frith 2004). A study of male Regent Bowerbirds *Sericulus chrysocephalus* that included both bower-owners and non-bower-owners found annual survival rates of 74 per cent (all ages) and 87 per cent (adults only) (Lenz 1999). By the end of my study, seven males had owned bower sites for at least seven years. Longer-term studies in other species have recorded the same individual at a bower site for up to 20 years (Frith and Frith 2004).

Given the high population density of Great Bowerbirds in Townsville, and the year-round availability of food and water (Frith *et al.* 1996; Doerr unpub. data), it is somewhat surprising that survival rates were not higher. The estimate of survival rate is similar to that of other species, but it is also the lowest recorded for bower-owning males. It is possible that survival rates were relatively low because some males left the study site to build bowers elsewhere. Although it is uncommon for established males to abandon their bower sites, even in areas with considerable disturbance from humans (Frith *et al.* 1996; Frith and Frith 2004), males in their first year of ownership frequently experience bower destruction from their neighbors, which may cause them to abandon their bowers (Borgia and

TABLE 1

Survival rates of bower-owning male Great Bowerbirds in Townsville from 2003 to 2007. Males that disappeared from their bowers were assumed to have died. For each column, deaths within breeding season = males that disappeared from their bowers between 1 September – 15 December of year 1. Deaths outside of breeding season = males that disappeared between 16 December – 31 August of year 2.

	2003-2004	2004-2005	2005-2006	2006-2007
Deaths within breeding season	1	1	1	0
Deaths outside of breeding season	5	4	1	7
Number of bowers monitored	28	34	30	27
% Survival rate (mean ± sd)	79 ± 8	85 ± 6	93 ± 5	74 ± 9

TABLE 2

Survival rates of male Great Bowerbirds according to years of bower ownership – see Methods (1). For each column: 'Number present, season 1' = males that were present at bowers during the breeding season of year 1 (1 September to 15 December). Some males were not present for the full breeding season, but they were still included in this tally; 'Number present, season 2' = males that returned to their bower sites the following breeding season. Males that did not return were assumed to have died.

	First year of ownership				Two or more years of ownership			
	2003-2004	2004-2005	2005-2006	2006-2007	2003-2004	2004-2005	2005-2006	2006-2007
Number present, season 1	7	7	1	3	18	22	29	23
Number present, season 2	5	5	0	1	14	22	28	18
Survival rate	61%				89%			

Gore 1986). Seven of the 20 males that disappeared over the course of this study were in their first year of ownership, and three experienced moderate to severe bower destruction (Doerr unpub. data). If these individuals left the study area in search of a site where they would experience less interference, then this could have biased the estimate of survivorship downwards. Indeed, when survival rates were calculated separately for different age classes, it was found that males in their first year of bower ownership had a survival rate of 61 per cent, while males that had been bower owners for two or more years had a survival rate of 89 per cent. Although the lower apparent survival rate of first-year males could have been the result of dispersion from the study site, younger males may also experience increased mortality (Newton 1989), so additional studies are needed to determine whether first-year males that fail to return the following season have died or dispersed. Previous studies in Tooth-billed and Golden Bowerbirds have documented survival rates for bower-owning males of all ages (reviewed in Frith and Frith 2004), but Borgia (1993) estimated the survival rate of Satin Bowerbirds based on males that owned 'permanent' bower sites. If his estimate excluded first-year males that did not reappear the following year, then this could have led to higher survival estimates than this study.

Alternatively, the results could indicate that male Great Bowerbirds within Townsville experience a slightly lower survival rate than other species. Though Townsville's year-round availability of food and water may enhance survivorship, the suburban environment may contain hazards that bowerbirds are not exposed to under natural conditions. Townsville males often build bowers in bushes along the side of roads and swoop low to the ground when approaching their bowers (Doerr pers. obs.). This may increase the likelihood that they will be killed by a vehicle. Over the course of the study, bodies of at least eight Great Bowerbirds were found that appeared to have been struck by vehicles on the study site, though none were the bower-owning males included in this study. An earlier study conducted at the same location in Townsville found one banded individual (sex unknown) struck by a car (Day pers. comm.).

Annual survival rate of bower-owning male Great Bowerbirds is generally consistent with the pattern of high survivorship found in other bowerbird species. However, future studies documenting survival rates in more natural populations of the Great Bowerbird are needed to determine whether Townsville males experience lower survival rates than do other populations and species.

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