Short Communications

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When Should Mayfield Model Data be Discarded?

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ABSTRACT.—Much confusion exists over the proper way to handle nest-fate data collected after the fledge date when using the Mayfield method. I provide a simple numerical example showing how use of these data can bias estimates of daily survival probability, and present a likelihood function demonstrating that nest-fate data collected after the fledge date do not contribute any information for parameter estimation, except in a seldom-realized special case. Consequently, it is recommended that under the Mayfield model, nest-fate data collected after the fledge date be discarded. *Received 16 April 2004, accepted 31 July 2004.*

Previously, I presented a generalization of the Mayfield method (Mayfield 1961, 1975) for estimating daily survival probabilities of nests, and advocated discarding nest-fate data collected after the fledge date of a nest (Stanley 2004). The reason for this recommendation is that errors or uncertainty in determining nest fate after the fledge date, combined with decisions by the investigator as to how these data should be handled, can unnecessarily bias estimates of daily survival probability. Because this problem also manifests itself in the widely used Mayfield model for daily survival probabilities, and because (in my experience) there continues to be confusion regarding when and why such data should be discarded (Manolis et al. 2000), I present in this note a simple numerical example illustrating the problem and how it can be avoided. My goal is to bring clarity to, and increase awareness of, this issue.

Let us suppose we have a population of 32 nests, each containing exactly one nestling, and that the daily survival probability (p) for those nests is 0.5 (these numbers were chosen for illustrative purposes, and are not intended to be realistic). Further, suppose that we know every nest is exactly 2 days from fledging, and that after the first day 16 nests survive and 16 fail, and after the second day 8 of the 16 remaining nests survive to fledging and 8 fail before fledging. Finally, of the eight nests that failed during the second day, assume that at four of the nests there was obvious evidence that the nest had been depredated (e.g., feathers, tissue remains), and at the remaining four nests there was no evidence (e.g., the nestling was carried off). If we were studying this population of nests and had perfect knowledge of the situation just outlined (except for p), then the likelihood function (L) under which we would estimate p would be proportional to $p^{16}(1 - p)^{16}p^{8}(1 - p)^{8}$ (Johnson 1979), and our maximum likelihood estimate of p would be $\hat{p} = (16 + 8)/(32 + 16) = 0.5$. This estimate is mathematically equivalent to the usual Mayfield estimate, and is unbiased.

Now consider a slightly different situation, where we have the same information as above except that we do not know the fate of every nest after the second day because when we arrived at nests they were empty. We are, however, able to correctly deduce that at least 4 of the 16 nests failed because there were feather and tissue remains and we knew the nests contained only one nestling. How should we analyze these data? I present three scenarios:

Scenario 1.—Because we found no evidence to the contrary, and because the nestlings were gone from the nest, we assume the 12 nests without evidence of predation successfully fledged young. Under this assumption we get $L \propto p^{16}(1 - p)^{16}p^{12}(1 - p)^{4}$, and $\hat{p} = (16 + 12)/(32 + 16) = 0.583$. This estimate is positively biased, because the true $p = 0.5$.

Scenario 2.—Because we only know with certainty that four nests failed after the second day, we only use those data in our analysis. This is equivalent to assuming there were only 4 nests at risk of predation the second day (instead of 16); therefore, $L \propto p^{16}(1 - p)^{16}p^{0}(1 - p)^{4}$, and $\hat{p} = (16 + 0)/(32 + 4) = 0.444$. This estimate is negatively biased.

Scenario 3.—Because we cannot determine

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unequivocally the fate of *every* nest checked after the second day (the fledge date), we discard all data for nests checked after the fledge date. Under this scenario we get $L \propto p^{16}(1 - p)^{16}$, and $\hat{p} = (16)/(32) = 0.5$. This estimate is unbiased.

Of the three scenarios presented, only the last yields an unbiased estimate of p. We were able to use data collected after the first day because we knew the nests were 2 days from fledging when they were found; hence, we knew the 16 empty nests found after the first day had to have failed. However, when we found 16 empty nests after the second day we could not be certain of the fate of every nest (only 4 of them). Consequently, it was necessary to discard all data from the second day so we would not bias our estimate.

The situation above, where knowledge of nest fate is imperfect, was simplified to illustrate the main point of this note. In reality, there are likely to be some nests checked after fledging where failure or success can be determined without error. If we let r_1 be the probability a nest checked after the fledge date is determined to have succeeded when it did, in fact, succeed, and let r_2 be the probability a nest checked after the fledge date is determined to have failed when it did, in fact, fail, then the appropriate model for our data (continuing with the example above) is

$$L \propto p^{n_1}(1 - p)^{n_2}(r_1 p)^{n_3}[r_2(1 - p)]^{n_4} \times [(1 - r_1)p + (1 - r_2)(1 - p)]^{n_5}.$$

Here, n_1 and n_2 are the number of nests surviving or failing after the first day, n_3 and n_4 are the number of nests known with complete certainty to have survived or failed over the second day (i.e., known-fate nests checked after the fledge date), and n_5 is the number of nests checked after the fledge date where fate could not be determined with complete certainty (in the preceding numerical example $n_1 = 16$, $n_2 = 16$, $n_3 = 0$, $n_4 = 4$, and $n_5 = 12$). Using standard maximum likelihood methods under the assumption that $r_1 \neq r_2$, it can be shown that the maximum likelihood estimate for p is $\hat{p} = n_1/(n_1 + n_2)$. In other words, none of the nest-fate data collected for nests after the fledge date (i.e., n_3, n_4, or n_5) contributes information to the parameter estimate, even though the fate of some of those nests is known with certainty. It is as if the data did not exist, or were discarded. Only in the special case where $r_1 = r_2$ (and r_1, $r_2 > 0$) do nest-fate data collected after the fledge date contribute to the estimate of p. In that case, $\hat{p} = (n_1 + n_3)/(n_1 + n_2 + n_3 + n_4)$. Because in real-world situations it will almost always be the case that $r_1 \neq r_2$, and because r_1 and r_2 will usually be unknown (so equality can not be ascertained), it is evident that nest-fate data collected after the fledge date should almost always be omitted from analyses under the Mayfield model (i.e., scenario 3 above). Attempts to use these data in an *ad hoc* fashion, as was illustrated by scenarios 1 and 2 above, will only serve to bias what would otherwise be an unbiased estimate.

In the material above, I have shown that even under ideal conditions—where nests are checked daily, the exact fledge date is known, and there is only one nestling per nest—nest-fate data collected after the fledge date do not contribute information for parameter estimation under the Mayfield model, and, if used in an *ad hoc* fashion, will introduce bias. In reality, the situation is even worse than I have portrayed. In most studies, nests are not checked daily and the exact fledge date is unknown. Consequently, evidence that might indicate nest fate (e.g., the presence of nearby young, tissue remains) will have had time to disappear, and we do not know how many days passed before the nest failed or fledged. Thus, we do not know the number of ‘‘nest days’’ to credit to a nest and this can create additional bias, even in the special case where $r_1 = r_2$. Furthermore, for many species there is often more than one nestling present and this will further complicate accurate assignment of nest fate. For example, suppose a nest contained three nestlings and that two fledged before the third nestling was taken by a predator. We would likely conclude the nest had failed, even though it actually succeeded. Once again, this can create additional bias. These real-world complications only serve to reinforce the main message of this paper, that nest-fate data collected after the fledge date—or more precisely, the predicted fledge date as determined by the investigator—should be omitted from the analysis.

The Mayfield model was developed under the assumption that daily survival probability

(p) is constant, when, in reality, p is probably heterogeneous (Stanley 2000, Dinsmore et al. 2002, Stanley 2004). If p is heterogeneous, and if the interval between nest checks is long, then it is possible that discarding nest-fate data collected after the fledge date will result in a loss of information about the nature of heterogeneity in p near the fledge date, and this could adversely affect robustness of the Mayfield estimator (D. H. Johnson pers. comm.). To prevent the loss of such information, investigators should make every effort to check nests more frequently as the predicted fledge date approaches. Not only will this lead to more robust estimates under the Mayfield model by decreasing the net information loss from discarded data, but it also will allow investigators to continually update the predicted fledge date so that in the end it more closely approximates the actual fledge date, thereby improving estimates.

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Predation of a Golden-cheeked Warbler Nest by a Western Scrub-Jay

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ABSTRACT.—I observed a Western Scrub-Jay (*Aphelocoma californica*) consume a Golden-cheeked Warbler (*Dendroica chrysoparia*) nestling and a Brown-headed Cowbird (*Molothrus ater*) nestling in northwestern Travis County, Texas, in May 1995. During a 4.5-hr period after brood destruction, warbler adults repeatedly brought insects to the depredated nest, and during each visit they appeared to search for the nestlings in the nest area and adjacent trees while carrying the insects. When the jay subsequently returned to the nest to take an unhatched egg, the female warbler performed a distraction display. My observations indicate that, in some cases, parental feeding behavior and nest defense can continue for a short time after brood loss. *Received 27 March 2002, accepted 28 May 2004.*

The Golden-cheeked Warbler (*Dendroica chrysoparia*) is an endangered species that breeds only in mature oak (*Quercus* spp.)-Ashe juniper (*Juniperus ashei*) forests or woodlands in central Texas. Nest predation is an important cause of mortality for this species (Gass 1996, Jette et al. 1998, Ladd and Gass 1999) and has been described in detail only for rat snake (*Elaphe guttata*) predation (Pulich 1976, Stake 2001) and Brown-headed Cowbird (*Molothrus ater*) predation (Stake and Cavanagh 2001). Documentation of parental behavior in response to predation is especially scarce. Here, I provide the first detailed account of nest predation at a Golden-cheeked Warbler nest by a Western Scrub-Jay (*Aphelocoma californica*) and describe warbler behavior in response to predation.

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I recorded this observation during a study of Golden-cheeked Warblers at the Balcones Canyonlands National Wildlife Refuge in northwestern Travis County, Texas (30° 30′ N, 97° 58′ W). The warbler nest was 3.2 m high in a 4.5-m high Ashe juniper on the south-facing slope of a sparsely wooded canyon. It contained one 3- to 4-day old Golden-cheeked Warbler nestling, one 4- to 5-day old Brown-headed Cowbird nestling, and one unhatched Golden-cheeked Warbler egg (L. Gass pers. comm.). I watched the nest for a total of 5 hr and 24 min from a distance of 10 m using a spotting scope and 8 × 42 binoculars.

On 16 May 1995 at 07:40 CST, an adult Western Scrub-Jay began foraging on the ground near the warbler nest, during warbler feeding visits. When it was 8 m from the nest tree, the jay stopped foraging and flew to a branch below the nest. After hopping from branch to branch for several seconds, the jay flew to the limb supporting the nest, and the nestlings began vocalizing with typical begging calls. The jay grasped the cowbird nestling by the neck and carried it to the ground. The jay vigorously pecked at the nestling several times and tore off and swallowed several chunks of flesh. My view was partially obscured, but I presume that the jay consumed the entire nestling, as no prey remains were later found at this location. Immediately afterwards, the jay returned to the nest, removed the warbler nestling, carried it to the ground, and consumed it in the same manner. The jay then returned to the nest a third time, picked up the remaining warbler egg, placed it back in the nest, and flew off. This series of events lasted about 2 min, during which the adult warblers were apparently unaware of the jay's presence. Five min later, the female warbler brought an insect to the nest, swallowed it immediately upon perching over the nest, consumed a fecal sac, and departed. The warbler did not appear to be alarmed during this visit. During the next 4 hr and 22 min, the adults brought insects to the nest seven times. They perched at the nest with food in their bills, uttered repeated ''chip'' notes (Pulich 1976), and swiftly hopped around the nest, nest branch, nest tree, and neighboring trees. I interpreted these behaviors as searching bouts, where the adults were apparently in search of their nestlings. Each bout lasted approximately 5–30 sec, totaling about 90 sec for the female and 40 sec for the male over the entire observation period. After each of these bouts, the warblers returned to the nest and either swallowed the insect they were carrying, or departed from the nest area with the food still in their bills. During three visits, the parents spent several seconds probing for and consuming fecal material from the bottom of the nest.

At 12:45, I again observed a Western Scrub-Jay (presumably the same individual) foraging on the ground near the nest. The warblers began chipping excitedly in the trees above the jay, and at 12:48, when the jay was foraging 15 m from the nest tree, the female performed a distraction display 3–4 m from the jay. With its tail feathers spread and wings fluttering, the warbler chipped rapidly and hopped gradually along a low branch. The jay did not appear to react to this display, and it continued foraging. At 12:50, the jay, 10 m from the nest tree, flew directly to the warbler nest and carried the remaining egg to a nearby branch. While the jay held the egg against the branch with its feet and began to consume the egg, the adult warblers chipped loudly close by. The jay did not appear to react to the warblers and several seconds later flew from the nest area. The warblers remained in the nest area and chipped loudly for 11 min, but no additional parental feeding bouts were observed. I stopped watching the nest at 13:15.

Whereas Western Scrub-Jays were considered likely nest predators of Golden-cheeked Warblers before this observation was recorded (U.S. Fish and Wildlife Service 1990), this is the first detailed description of Golden-cheeked Warbler nest predation by this species. (A summary of this observation is cited in Ladd and Gass 1999 as ''J. Petick [sic] pers. comm.'') Reported responses of adult Golden-cheeked Warblers to predators have included injury feigning displays, wing fluttering, agitated calling, flying away into the tree canopy, and remaining still or silent for prolonged periods (Ladd and Gass 1999; JP pers. obs.). The warblers' behavior during this predation event is noteworthy because of the repeated delivery of food to the depredated nest, the apparent bouts in search of young, and the distraction display following predation. These observations indicate that, in some cases, parental feeding behavior and nest defense can continue for a short time after brood loss.

I offer two possible explanations for the warblers' response to nest predation. First, the warblers' reaction may have been due to a strong residual parental feeding instinct that continued for a short time after nest failure. This behavior is not uncommon (Welty and Baptista 1988) and, in fact, other bird species have been observed feeding the young of other broods of the same or different species, when their own brood has been destroyed (e.g., Shy 1982, Stafford 1986). Second, since the warblers did not appear to detect the jay near the nest during the removal of the two nestlings, their behavior may have been an attempt to locate, feed, and defend young that could have fledged from the nest while the adults were absent. The nestlings were about 4 days away from fledging, but adult warblers may not be able to accurately predict the timing of this event. Instead, adult warblers may begin the fledgling phase of parental care when they notice that the nestlings are absent from the nest, even if this absence is due to predation.

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Age Differences in Wing Loading and Other Aerodynamic Characteristics of Red-tailed Hawks

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ABSTRACT.—We examined age differences in wing loading, aspect ratio, wing span, and tail area in a sample of 117 Red-tailed Hawks (*Buteo jamaicensis*) captured at the Cedar Grove Ornithological Station, Wisconsin, during 1979–1987. Adults had significantly wider wings, lower aspect ratios, shorter tails, and smaller tail surface areas than juveniles. Red-tailed Hawks showed fewer age differences in aerodynamic characteristics than Sharp-shinned Hawks (*Accipiter striatus*), probably because of differences between the two species in the pursuit and capture of prey. Sharp-shinned Hawks take birds from above ground or after a brief chase, often in dense vegetation. Sharp-shinned Hawks require more aerial agility (ability to make rapid twists and turns) than is necessary for Red-tailed Hawks, which capture prey on the ground, usually after a glide or flight from an elevated perch. *Received 7 July 2003, accepted 6 August 2004.*

Wing area, wing loading, and other aerodynamic characteristics are especially important for those diurnal birds of prey that spend considerable time on the wing and rely on agility in flight for capturing prey. There are few data on aerodynamics for species of Falconiformes; of the data that do exist, they may include only a single specimen, and often age is not noted (Mueller et al. 2002). We examined age differences in wing loading and other aerodynamic characteristics of Red-tailed Hawks (*Buteo jamaicensis*) based on a sample of 117 wings and 89 tails. We captured the hawks during fall migration 1979–1987 at the Cedar Grove Ornithological Station (43° 33′ N, 87° 21′ W) on the western shore of Lake Michigan in Sheboygan County, Wisconsin. The hawks were trapped in bow-nets or dhogazzas (Bub 1991).

We previously explained in detail (Mueller et al. 1981) the methods used to obtain our data. Briefly, we held up the extended wing (or tail) against a vertical sheet of Plexiglass ruled into 5-cm squares and photographed it. Subsequently, we projected each negative to one-half life size on a sheet of paper and drew an outline of the wing and the adjacent body (or tail). We measured the area of each drawing with a compensating polar planimeter. Measurements were taken as in Mueller et al. (2002): wing surface area is the area of both wings plus the area of the adjacent body; wing loading is mass divided by wing area; flight surface area is wing surface area plus tail surface area; flight surface loading is mass divided by flight surface area; wing span is 2× wing length plus the distance across the adjacent body; and aspect ratio is the square of the wing span divided by wing surface area. Using SYSTAT for Macintosh (Wilkinson 1989), we conducted *t*-tests for all comparisons.

Tail surface area varies greatly with how much the tail is spread. We used the following formula to estimate tail area, using only angle of spread and tail length:

$$\text{Area} = (A/360)\,(\pi B^2 - \pi C^2),$$

where A is the angle formed by lines drawn along the two outer rectrices until they meet on a drawing made from a photograph of the tail, B is the distance from the apex of this angle to the tip of the longest rectrix, and C is B minus the tail length measured on the live bird. Regression of C on A yields $C = -0.11A + 16.64$, $R^2 = 0.67$, $P < 0.001$. The surface area thus estimated is an excellent fit to the measured area (adults $R^2 = 0.85$; juveniles $R^2 = 0.89$; both $P < 0.001$).

Juveniles had significantly narrower wings,

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higher aspect ratios, and longer tails than adults (Table 1). The angle of spread of the photographed tails did not differ between juveniles and adults, and at an angle of about 65° juveniles had significantly greater tail surface areas (12.8%) than adults. The difference in tail area ranged from 9.7% in a mostly folded tail (spread 15°) to 13.4% in a fully fanned tail (130°).

There were no significant differences between juveniles and adults in mass, wing loading, or flight surface loading (wing and tail). However, adults had greater mass than juveniles in a larger sample taken during 1963–1999 ($t = 8.64$, df $= 4{,}398$, $P < 0.001$). Wing surface areas were not measured in the 1963–1999 sample, but age differences in wing loading might exist.

Adults thus had shorter tails, lower aspect ratios, and wider wings than juveniles. The tail of a bird serves a vital function during landing, when it is spread and thrust forward: it deflects air downward over the wings, thus increasing lift and preventing a stall (Pennycuick 1985). This effect would be particularly useful in the high speed ''landing'' when a hawk strikes prey on the ground. The larger tails of juveniles aid these inexperienced birds in striking prey. The wider wings of adults may help compensate for their shorter tails. The higher aspect ratio in juveniles makes them more efficient in soaring flight but at the expense of a loss in maneuverability, which is compensated for by an increase in tail area.

Red-tailed Hawks strike their prey on the ground, usually after a glide or flight from an elevated perch (Preston and Beane 1993). Mammals are the hawks' most common prey; during a predation attempt, the maximum aerodynamic constraints a hawk incurs are probably in braking just before the prey is struck. Sharp-shinned Hawks (*Accipiter striatus*) show more age differences in aerodynamic characteristics than Merlins (*Falco columbarius*), which in turn show more differences than Red-tailed Hawks. Sharp-shinned Hawks capture perched birds, often in dense vegetation, or in flight after a brief chase (Bildstein and Meyer 2000). Merlins usually capture birds in the air, often after a series of stoops at a flight speed considerably greater than that of Sharp-shinned Hawks (Sodhi et al. 1993). The tail and wings are used to deflect the airstream in rapid twists and turns. The force produced by such a deflecting surface is proportional to the area of the surface and the square of the airspeed. A falcon in rapid flight needs less deflecting surface than a hawk en-

TABLE 1. Wing chord, wing loading, and other characteristics of Red-tailed Hawks captured during fall migration at Cedar Grove Ornithological Station, Wisconsin, 1979–1987.

	Adults (n = 52)		Juveniles (n = 65)			
	Mean	SD	Mean	SD	t	P[a]
Wing chord (cm)	38.2	1.75	38.4	1.75	0.78	1.00
Wing length (cm)	54.2	2.86	54.8	3.07	1.07	1.00
Wing width (cm)	19.4	1.06	18.7	0.96	3.31	0.01
Wing span (cm)[b]	122.0	5.75	122.5	6.44	0.42	1.00
Aspect ratio[c]	6.31	0.34	6.54	0.30	3.95	0.001
Wing surface area (cm^2)[d]	2364.1	212.9	2298.8	214.5	1.04	1.00
Mass (g)	1083.8	152.8	1064.5	162.4	0.66	1.00
Wing loading (g/cm^2)[e]	0.458	0.049	0.462	0.049	0.44	1.00
Tail length (cm)	21.1	0.96	22.7	1.01	7.30	0.001
Tail angle (degrees)[f]	66.8	12.22	63.4	18.82	0.74	1.00
Tail surface area (cm^2)[g]	440.4	59.66	496.6	85.83	3.49	0.001
Flight surface area (cm^2)[h]	2804.5	212.93	2795.4	214.98	0.23	1.00
Flight surface loading (g/cm^2)[i]	0.386	0.041	0.380	0.042	0.79	1.00

[a] Bonferroni corrected probabilities.

[b] 2× wing length plus the distance across the adjacent body.

[c] Wing span^2/wing surface area.

[d] Area of both wings, plus the area of the adjacent body.

[e] Mass divided by wing area.

[f] Angle of spread of the tail. The sample size for tail measurements is 39 adults and 50 juveniles.

[g] Tail surface area at 65° angle of spread.

[h] Wing surface area plus tail surface area.

[i] Mass divided by flight surface area.

gaged in slower twists and turns. Compared with Sharp-shinned Hawks and Merlins, the minimal age-related differences in control surfaces of Red-tailed Hawks may result from a reduced need for them. The variation between species in age differences in aerodynamic characteristics is attributable to differences in hunting methods.

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Breeding Ecology and Nesting Success of Abbott's Babbler (*Malacocincla abbotti*)

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ABSTRACT.—Baseline demographic data are lacking for most tropical forest birds, particularly from undisturbed habitats. During the 2003 breeding season, we documented the productivity of Abbott's Babbler (*Malacocincla abbotti*), a sedentary insectivorous passerine, on a 30-ha permanent forest plot in northeastern Thailand. We found 17 active nests of 13 breeding pairs, for which the Mayfield estimate for overall nesting success was 0.36 ± 0.13 SE. Breeding started in mid-January, a month earlier than previously recorded. Despite a relatively long period of post-fledging parental care, at least five pairs were double-brooded.

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The breeding ecology and nesting success of many tropical birds is generally unknown (Robinson et al. 2000, Stutchbury and Morton 2001). In Asia, documentation, if any, often only describes the first known nesting, or unusual nesting behavior. Detailed demographic information on tropical birds from relatively undisturbed forest is essential for elucidating questions related to the evolution of life history characteristics, such as clutch size, number of broods, and nest success (Robinson et al. 2000), while at the same time serving as baseline data for assessing how species may respond to the rapid deforestation in the region (Lambert and Collar 2002, Food and Agriculture Organization of the United Nations 2003). We present information on the breeding ecology of Abbott's Babbler (*Malacocincla abbotti*), collected during an intensive study of forest birds in northeastern Thailand.

The Abbott's Babbler is a small, sedentary passerine that ranges from Nepal and northeast India through south-east Asia to Sumatra and Borneo. In Thailand, it is fairly common in the understory of broad-leaved evergreen forest and secondary growth up to 915 m in elevation (Robson 2000). Abbott's Babbler is socially monogamous with monotypic plumage. Males are larger than females (flattened wing chord: 75.3 mm ± 1.24 SE, $n = 21$, and 72.8 mm ± 0.80 SE, $n = 14$, respectively; AJP unpubl. data).

METHODS

Data were collected from January to June 2003 on the 30-ha Mo-singto permanent forest plot, Khao Yai National Park, Nakhon Nayok Province (14° 26′ N, 101° 22′ E). The plot was situated in mature, seasonally-wet evergreen forest at 723–817 m in elevation (Brockelman 1998). The vegetation was undisturbed except for a 20 × 120 m strip of approximately 40-year-old secondary forest at the northern edge of the plot. The average annual rainfall is 2,326 mm, most of which falls between May and October (Kitamura et al. 2002).

We conducted intensive searches to locate nests and breeding pairs of Abbott's Babblers. Nest contents were checked every 2–5 days to estimate laying, hatching, and fledging dates. We caught adult birds in mist nets using song playback or by placing nets near nests after eggs had hatched. Nestlings were banded 6–8 days after hatching. We banded all birds with one aluminum, Thai Royal Forest Department-numbered band and 2–3 color bands to allow individual recognition in the field. We calculated nesting success (incubation and nestling periods) following Mayfield (1961); standard errors were calculated following Hensler (1985).

RESULTS AND DISCUSSION

We found 13 pairs of Abbott's Babblers nesting on the plot; of those, 21 individuals were banded. At least one member of each pair was banded such that each nest could be assigned to a known pair. The banded male of

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TABLE 1. Mayfield estimates for nest success of Abbott's Babbler at Khao Yai National Park in northeastern Thailand, January–June 2003. Exposure days were terminated at the mid-points between the last observed active and the first observed inactive dates (Mayfield 1961). All nests in the calculations were of known outcome.

	Incubation period (n = 10 nests)	Nestling period (n = 12 nests)	Total (n = 17 nests)
Duration in days	17.75[a]	11[b]	28.75
Failed nests	1	7	8
Exposure days	98	96	194
Daily nest survival	0.990	0.927	0.966
Nest success[c]	0.834	0.435	0.362
Standard error[d]	0.152	0.137	0.133

[a] n = 6 nests, starting from first egg date following Robinson et al. (2000).

[b] n = 4 nests.

[c] Expected nest success based on daily survival rate.

[d] Calculated following Hensler (1985).

one pair disappeared after a failed nesting attempt and was replaced by an unbanded bird that did not breed. All other banded individuals remained paired in their territories throughout the study.

We found 17 active nests (8 first nests and 9 renests) of 6 pairs. The renests represented a range of 1–3 additional attempts. Fifteen nests were in rattan palms (*Calamus* spp.) and two were in small unidentified saplings (KP unpubl. data). We found nests from early February to late May, with young fledging from the last nest on 12 June. Two pairs with fledged young on 8 and 9 February, respectively, indicated that egg-laying began in mid-January. This extends by 1 month the previous estimated start date of the nesting cycle (Robson 2000). Clutch or brood size was three in all but one nest, which was found with two nestlings about 8 days old.

One egg was laid per day and incubation (female only) started the day after the clutch was complete. Of 28 eggs monitored, only 1 failed to hatch. Ten successful nests fledged 29 chicks. The incubation period was 14–15 days (mean = 14.75, n = 6) and nestlings fledged 10–12 days after hatching (mean = 11, n = 4). The Mayfield estimate for overall nest survival was 0.36 ± 0.13 SE (Table 1). Nest predation, and not desertion, appeared to be the main cause of nest failure; when it occurred, all contents of the nest were depredated. Although we had no direct observations of predation events, potential predators could have included a variety of other bird species, squirrels, snakes and pig-tailed macaques (*Macaca nemestrina*).

Because the adults were uniquely color-banded, we were able to document that at least five pairs (38%) were double-brooded—i.e., initiated a second nest after having already fledged young from a previous nest, following the definition of Ogden and Stutchbury (1996). For two of these pairs, at least part of their first brood was observed alive, and still dependent on the male, when the second nest was started. Eggs in both second nests hatched and the females attempted to raise their second broods alone; however, both nests failed due to predation. The first eggs of these two second broods were laid 49 and 64 days after first broods fledged. In a third pair, the second nesting attempt was initiated 46 days after the first brood fledged and 10 days after the fledged young were last known to be alive. In the remaining two pairs, first-brood fledglings disappeared within 2 weeks of fledging and presumably died prior to the second nesting attempts.

Our study represents one of the few detailed studies of the breeding biology of a Southeast Asian forest bird. Fogden's (1972) groundbreaking and widely cited study conducted in Sarawak, Malaysia, suggests that species that provide extensive post-fledging parental care (>10 weeks) do not have sufficient time for double-brooding during a normal breeding season. Our data suggest that Abbott's Babblers regularly care for young for 7–9 weeks or more after fledging, and yet are still able to double-brood—enabling them to potentially increase reproductive output (Holmes et al. 1992, Ogden and Stutchbury 1996).

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First Nest Description for the Ocellated Antbird (*Phaenostictus mcleannani*)

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ABSTRACT.—We present the first description of a nest of the Ocellated Antbird (*Phaenostictus mcleannani*), an understory species that ranges from southeastern Honduras to northwestern Ecuador. The open-cup nest was found in June 2002, in the Republic of Panama, and was located on the leaf litter between the buttresses of a *Virola surinamensis* tree. The nest contained two ovoid, whitish eggs with reddish-brown speckles and longitudinal streaks. *Received 20 January 2004, accepted 3 August 2004.*

The Ocellated Antbird (*Phaenostictus mcleannani*) is a ''professional'' army ant follower (*sensu* Willis 1973) that ranges from southeastern Honduras to northwestern Ecuador (Ridgely and Gwynne 1989, Zimmer and Isler 2003). In the Republic of Panama, the Ocellated Antbird is widespread throughout the undergrowth of lowland humid forests and has been recorded at elevations of up to 900 m (Ridgely and Gwynne 1989). Ocellated Antbirds, along with Bicolored Antbirds (*Gymnopithys leucaspis*) and Spotted Antbirds (*Hylophylax naevioides naevioides*), form the core of ant-following assemblages in central Panama (Willis 1973). The Ocellated Antbird is the least common of the three species, is relatively secretive, and is rarely observed away from swarms of army ants (Willis 1973). The natural history of this group is of interest due to its notable vulnerability to habitat fragmentation and isolation; for example, the Oc-

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ellated Antbird became extirpated from Barro Colorado Island in the 1970s (Karr 1982, Robinson 1999). Despite intensive studies of their ecology and behavior (Willis 1973), no confirmed observations of Ocellated Antbird nests have been previously reported. Here, we present what we believe is the first description of this species' nest.

We studied the reproductive ecology of birds on a 104-ha study area (see Robinson et al. 2000 for a full description of the study area) in the lowland forests of Soberania National Park in the Republic of Panama (9° 10′ N, 79° 45′ W). On 26 June 2000, while checking the buttresses of a medium sized *Virola surinamensis* tree (Family Myristicaceae: ~20 m high, 0.80 m diameter at base of buttresses, and 0.25 m diameter at breast height), AIC flushed an adult Ocellated Antbird and discovered a cup nest built amid the leaf litter on the ground between two of the tree's buttresses. The nest tree was located in forest 60–120 years old (Robinson et al. 2000).

We revisited the nest site on 27 June and measured the nest and eggs. The nest was set on the ground litter and was attached at the rim to the tree buttresses with fungal rhizomorphs (*Marasmius* spp.). The nest itself was a tightly knit cup made from fine fungal rhizomorphs and dried leaves. We did not observe additional lining material. The interior of the cup measured 85 mm in width and 40 mm in depth. The eggs were ovoid and whitish, speckled with reddish-brown spots and longitudinal streaks, much like Bicolored Antbird eggs (Stiles and Skutch 1989). The eggs weighed 5.0 and 4.9 g and both measured 27 mm in length and 20 mm in width at the widest point.

We revisited the nest every 3 days. The nest contained two eggs on 30 June, and on 3 July, we observed two naked hatchlings; their eyes were closed. By 6 July, the hatchlings had feather sheaths, and by 9 July, they were downy and their eyes had opened. On 15 and 16 July, the nest was intact but empty. Although we did not directly observe whether the nestlings fledged successfully or were depredated, a nestling period of approximately 12 days is common for open-cup-nesting antbirds (Willis 1972, Stiles and Skutch 1989).

The nest we observed was similar to descriptions of putative Ocellated Antbird nests presented by Willis (1973) and Zimmer and Isler (2003). We believe that our observations confirm the Willis (1973) and Zimmer and Isler (2003) nests as those of the Ocellated Antbird.

Most other species in the families Thamnophilidae and Formicariidae attach their open-cup nests to horizontal forks of shrubs or trees (antshrikes, antvireos, some antwrens and antbirds), or build in a hollow or cavity (some antbirds and antthrushes). The Ocellated Antbird's placement of a cup nest on the ground between tree buttresses makes it somewhat unique in these families (Stiles and Skutch 1989, Cadena et al. 2000). Species in the ecologically similar genus, *Phlegopsis*, place their nests inside hollow tree stumps (Cadena et al. 2000). A two-egg clutch is standard for open-cup nesters in the humid tropics (Skutch 1985).

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