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NATURAL HISTORY AND BEHAVIOR OF THE ALDABRA RAIL (*DRYOLIMNAS* [*CUVIERI*] *ALDABRANUS*)

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ABSTRACT.—The Aldabra Rail (*Dryolimnas* [*cuvieri*] *aldabranus*) is endemic to Aldabra Atoll, Seychelles and is the last remaining flightless bird in the tropical western Indian Ocean. We studied it over two breeding seasons from 1999 to 2001. Pairs formed strong bonds, defended territories year-round, and were mate and territory faithful across seasons. Reproductive duties are shared by males and females. Breeding was closely tied to the rainy season and pairs responded to favorable conditions by increasing clutch size and clutch frequency. Clutches contained 1–4 eggs and replacement clutches were laid if nests failed early in the season. The incubation period was 19–24 days and hatching was usually synchronous. Mayfield estimates of daily survival of eggs and nesting success were 98.8% and 77.0%, respectively. Hatching success was 60.9% and 57% of chicks that hatched were successfully reared to independence. Chicks are sub-precocial and fledged chicks were cared for in the natal territory for at least 2 months, after which they were forcibly evicted. A large repertoire of behaviors and ritualized displays are described including pseudo-copulation and reverse mounting. *Received 25 August 2006. Accepted 30 March 2007.*

The Aldabra Rail (*Dryolimnas* [*cuvieri*] *aldabranus*) is endemic to Aldabra Atoll, Seychelles. Historically, distinct representatives of the genus *Dryolimnas* occurred throughout the Aldabra Group (Aldabra and Cosmoledo atolls and Astove and Assumption islands), as well as on Madagascar and the Mascarenes (Rand 1936, Rountree et al. 1952, Benson 1967, Mourer-Chauviré et al. 1999). Only the White-throated Rail (*D. c. cuvieri*) of Madagascar and the Aldabra Rail remain—all other forms are extinct. The Aldabra Rail is truly flightless (Wanless 2003a) unlike its sister taxon on Madagascar (Rand 1936, Taylor and van Perlo 1998). The range of the Aldabra Rail had contracted by the 1970s to two islands within Aldabra (Malabar and Polymnie) and the small lagoon islet of Île aux Cèdres (Benson and Penny 1971, Collar 1993, Taylor and von Perlo 1998).

A reintroduction of Aldabra Rails to Picard Island was successfully undertaken in 1999 (Wanless et al. 2002). This provided the opportunity to study the natural history and breeding biology of the Aldabra Rail. The species received some research attention in the 1970s, but the autecological study went unpublished (Huxley 1982). We located the manuscript and received permission (C. R. Huxley, pers. comm.) to use the results to corroborate many of our findings, particularly those relating to pair behaviors. The objectives of our paper are to describe aspects of the natural history of the Aldabra Rail, including adult, juvenile, and chick plumages. We also describe use of a reliable genetic technique for ascertaining gender of Aldabra Rails, and a suite of territorial and reproductive behaviors and displays.

METHODS

Study Area.—Aldabra Atoll (9° 24′ S, 46° 20′ E) is 1,100 km southwest of the granitic Seychelles and 400 km north of Madagascar. It is a large, slightly raised coral atoll (34 × 14.5 km, land area = 155 km²). Four large islands (Grande Terre, Malabar, Picard, and Polymnie) form a rim around a substantial, shallow lagoon that contains numerous islets (Fig. 1). The climate is dry and tropical with an average annual temperature of 27° C. Annual rainfall is variable, but averages about 1,200 mm with a pronounced wet season, usually November–April (Stoddart 1971). The vegetation is low and either dense or open mixed scrub. The former includes large, almost monospecific stands of *Pemphis acidula*. Aldabra Rails were studied mainly on Malabar and Picard islands between 1999 and 2001.

Identification of Gender.—The method for gender identification in the field using bill color (Penny and Diamond 1971) proved unre-

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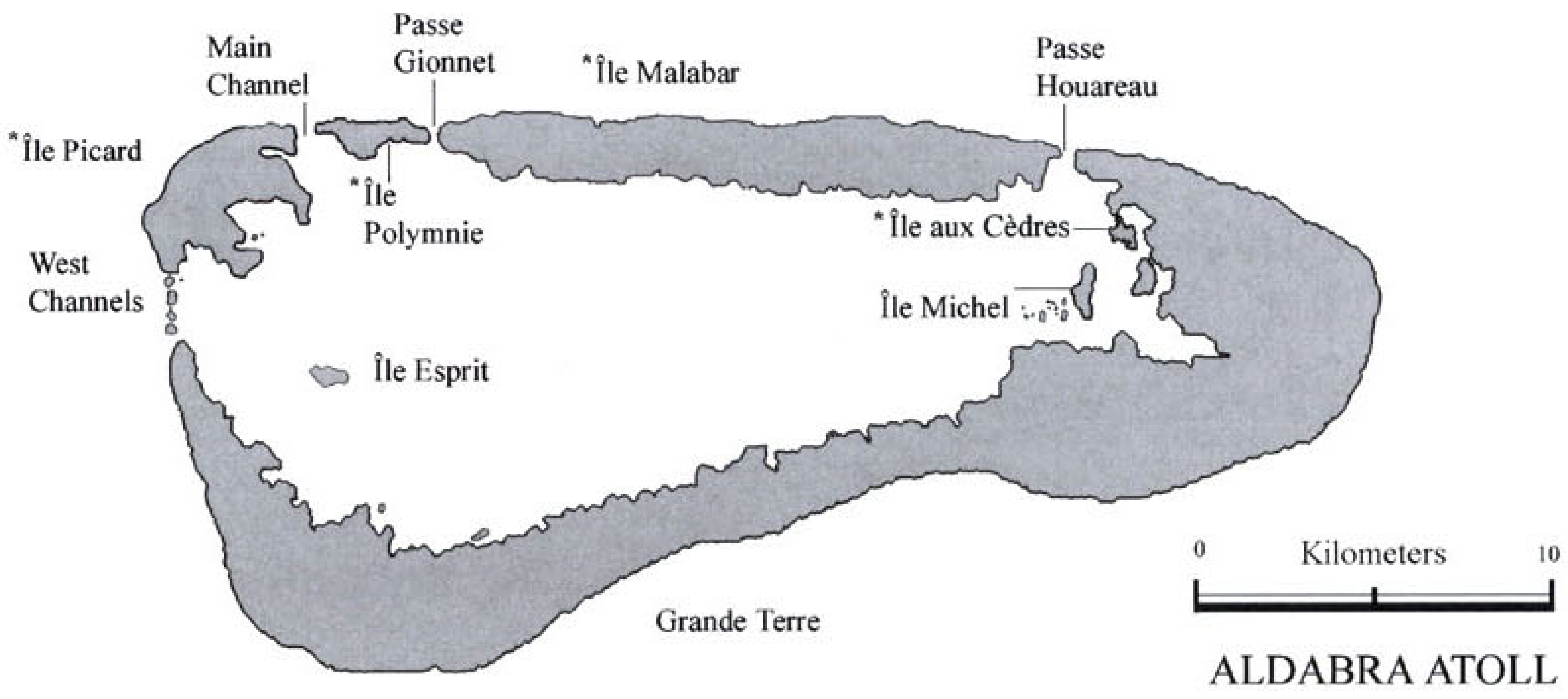

FIG. 1. Aldabra Atoll, Seychelles, showing the four rimming islands, larger lagoon islets, and the four channels to the open sea. Islands with Aldabra Rail populations are marked with asterisks.

liable based on necropsy of birds. We used a universal genetic technique (Fridolfsson and Ellegren 1999) to assign gender to all individuals that were trapped and banded. PCR blanks and positive controls were included to ensure reliable reactions. We compared bill and tarsus length measurements from 22 males and 22 females to investigate sexual dimorphism. Differences were tested with a t-test at the 0.05 significance level. Gender of birds was also assigned when handled following Penny and Diamond (1971), and the results were compared to with genetic identification.

Breeding Biology.—The location and construction materials of 23 active Aldabra Rail nests and the dimensions of nine were recorded. Elevation was measured from the ground to the base of the nest. Nest length (longest axis) and width were measured to the nearest 5 mm across the centre of the cup. Cup depth was measured vertically from the deepest part of the nest to the cup rim.

Eggs were measured to the nearest 0.1 mm using vernier callipers and weighed to the nearest 0.5 g using a 100 g Pesola spring balance. Many eggs were of unknown age and weights should be treated with caution.

Average clutch size was estimated from nests visited at least twice during incubation. In instances when nests were not found, but newly hatched chicks were located, a minimum estimate of clutch size was assumed to equal the number of chicks. The response of birds to favorable conditions was examined by comparing clutch size and number of repeat clutches between the reintroduced population on Picard (no density-dependent constraints on reproduction) and on Malabar (high density-dependence) (Wanless et al. 2002). Where appropriate, means ± one standard deviation are presented.

We performed a Kaplan-Meier survival function analysis (which calculates the cumulative proportion of nests surviving over time) for the incubation period with survival censored at 20 days (Nur et al. 2004). Hatching success was calculated from complete clutches only. We estimated the daily survival rate for eggs and nest success for the incubation period following Mayfield (1975): daily survival = 1 − *losses*/*e* and nest success = (daily nest survival)^{ip}, where e = exposure, the total number of active days per egg/nest, and ip is the incubation period. A nest was defined as successful if at least one chick fledged. We considered chicks in full juvenile plumage and capable of foraging for themselves to have been reared to independence. Chick survival is the number of chicks reared to independence divided by the number that hatched and breeding success is the number of chicks reared to independence per nesting attempt.

Behavior.—We took detailed notes in the field describing interactions between birds. Particular attention was given to posture and the role of the white throat patch and undertail coverts in displays. Birds were also photographed in various postures from which line drawings were produced. Interactions were either common (e.g., pairs duetting and greeting) or only seen opportunistically (e.g., mating). Consequently, no attempts were made to quantify the relative frequency or individual variation of behaviors, but Huxley's (1982) findings were incorporated or used to corroborate our observations.

RESULTS

Structure and Plumage.—The Aldabra Rail is a medium-sized rail with somewhat reduced wings that do not extend beyond the tail at rest. The body is slender, emphasized by the noticeable reduction of breast musculature. The upper parts are a dark, olive green, and the white throat patch contrasts strongly with the dark body plumage. The undertail coverts are also white. The bill is black, long, slender, and sharply pointed with the base variably pink or red. The head, neck, and breast of adults from Malabar and Polymnie are rich, dark, and red-brown with the flanks barred with white. Adults from Île aux Cèdres are noticeably duller, paler, and tinged with pink.

Newly hatched chicks are typical of rallids, being thickly covered with black down. Primary feathers begin to emerge from their sheaths at about 2 weeks. Juveniles resemble adults but are duller with reduced contrast between upper and lower body coloration.

Identification of Gender.—The gender of 47 (81%) of 58 adults ascertained in the field was confirmed to be correct by genetic analysis; of the remaining 11 birds, six males were incorrectly identified as females and five females as males. Males were significantly larger than females in bill length (43.5 ± 2.7 vs. 39.4 ± 1.5 mm, df = 42, $P < 0.001$) and tarsus length (45.4 ± 5.7 vs. 41.3 ± 1.3 mm, df = 42, $P = 0.007$). However, there was overlap between large females and small males in both measures (Fig. 2), and we conclude that gender of Aldabra Rails cannot be reliably identified in the field or in the hand.

General Ecology.—Paired birds roosted on the ground, usually less than 10 m apart, and were diurnal becoming active at first light by immediately performing a duet. This was frequently echoed by other nearby pairs in a

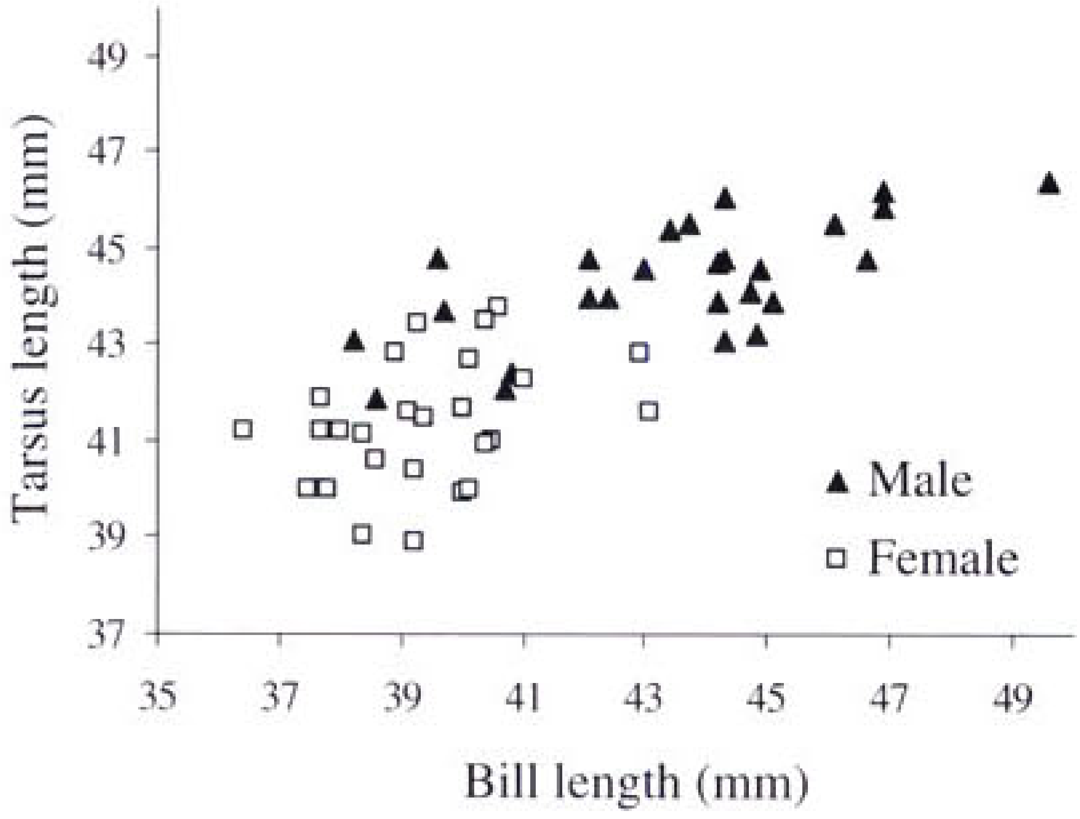

FIG. 2. Sexual dimorphism in correlated morphological characters of the Aldabra Rail from 22 adult females and 22 adult males.

domino effect. Occasionally, birds called or pairs duetted in the middle of the night.

Aldabra Rails use their bills to remove leaf litter, probe soil, and catch food; the feet were not used to scratch in litter or to manipulate food. Size of prey items was, in most cases, too small to estimate and no identifiable remains were found in fecal samples. A single regurgitation contained finely crushed arthropod exoskeleton(s) and 18 tiny land-snail shells. The latter might have been ingested as grit to aid digestion. Aldabra Rails hunted geckos, skinks, and crabs opportunistically. These prey were held in the bill when captured, while the bird alternately flicked its head rapidly from side to side and then beat the prey against the ground or a branch. Larger crabs were killed by rapid, powerful blows with the bill directed between the eyes. Crab exoskeletons and hermit crab shells were broken open by placing them on the ground and repeatedly hammering them from above. Rails washed large food items if water was nearby.

Breeding Biology.—Courtship behavior prior to pair formation has not been reported. New pair formation occurred within 5 days after reintroduction to Picard Island, but could have happened earlier. Aldabra Rails are monogamous and both males and females defended the territory year-round. Territory fidelity between years was high; of 14 pairs on Picard Island where both individuals were color-banded, only two pairs were suspected of having shifted territory. Males and females shared incubation and chick-provisioning du-

TABLE 1. Clutch sizes and breeding success (defined as chicks reared to independence per nest) of Aldabra Rails. ND denotes no data.

Parameter	Total nests (eggs)	Mean clutch size	Total hatched	Chick survival	Breeding success
All clutches (Picard and Malabar)	23 (65)	2.83	ND	ND	1.11
All clutches (Picard only)	17 (51)	3.0	30	20	1.05
First clutches (Picard only)	9 (28)	3.11	21	14	1.27
Repeat clutches (Picard only)	8 (23)	2.88	9	6	0.75

ties. There was no evidence of cooperative breeding in the species and young were invariably evicted from the natal territory, usually at 8–10 weeks of age, once they had attained full juvenile plumage.

The most conspicuous pair behavior was the duet, which consists of a series of loud, high-pitched, ascending whistles that increase in pitch to a sustained crescendo. Duets were given after a territorial dispute, after the *Greeting Display*, or in response to other pairs duetting nearby. We interpret duetting as an integral part of pair-bonding behavior. Pair-bonding activities were increasingly noticeable as the breeding season approached. Duetting and response to playback of duets were noticeably reduced during chick rearing, and other pair-bonding behaviors were seldom seen.

Nesting Ecology.—Nest site prospecting began in November or early December and males did most of the building. Two or more nests may be built and material was often placed in several potential sites. Once a site was selected, one or both birds stood on or near the site and gave a series of low, groaning *crreaak* calls.

Eight of 23 active nests were on the ground; the other 15 were in low shrubs, *Pandanus tectorius* bushes, or natural cavities in trees. Elevated nests ranged from barely above ground to 1.6 m above ground (mean = 0.8 m, n = 14). Only 1 of 23 nests lacked some overhead shelter.

A wide diversity of dry plant material (usually the dominant litter of the area) was used in nest construction. Two active nests, however, had almost no added material and were natural depressions (under a shrub and in a tree cavity, respectively), sparsely lined with dry grasses or *Casuarina* needles.

Nests were usually constrained by the nature of the site, but most were quite large and roughly circular (260 ± 33 × 221 ± 22 mm, n = 23). The mean depth was 116 ± 61 mm (n = 9). The mean cup length was 149 ± 22 mm, mean width was 134 ± 27 mm and the mean depth was 48 ± 24 mm (n = 9 for all cup measurements). The cup was usually sufficiently deep that only the head of an incubating adult protruded; the adult's black-streaked, dull olive-green back camouflaged it well on the nest. Three pairs used brooding nests to brood downy chicks; others may have gone undetected. These were built on the ground under shelter and consisted of a shallow cup lined with a thin layer of dry material.

Mean egg dimensions were 43.3 ± 1.2 × 30.6 ± 1.1 mm, and mean mass was 21.4 ± 2.1 g (n = 39). Eggs varied in shape, but most were elliptical or biconical. The moderately glossy, off-white shell is covered in maroon-brown speckling and has a finely granulated surface. Speckling is most dense at the obtuse end and many speckles are clouded or adumbrated, giving a multi-toned appearance.

Twenty-three clutches were monitored from egg-laying or incubation to completion (Table 1). Small unequal sample sizes and the non-independence of samples (repeat clutches) prevented testing for differences in mean clutch size between the reintroduced population from Picard and the source population on Malabar. Average clutch sizes were slightly larger on Picard (3.0, range 2–4 eggs, n = 17) than on Malabar (2.33, range 1–3 eggs, n = 6). Excluding repeat clutches increased mean clutch size on Picard to 3.11 eggs (n = 9 nests).

Six pairs on Picard attempted second clutches after successfully rearing chicks, four of which were successful. Two pairs laid third clutches, both of which failed at the egg stage (Guy Esparon, pers. comm.). A pair on Malabar in 2000/2001 built a new nest and laid immediately after their first clutch was dep-

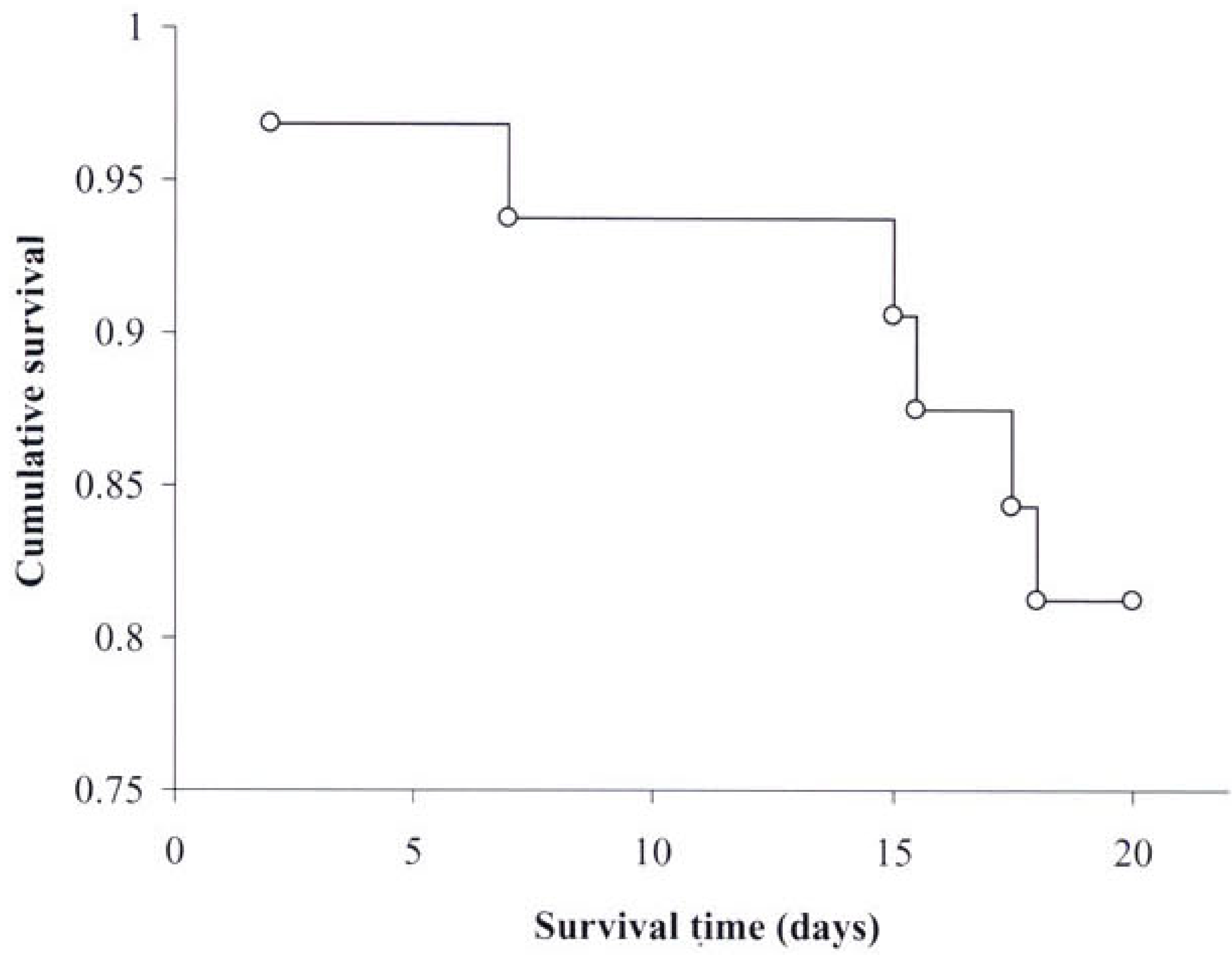

FIG. 3. Kaplan-Meier survival probabilities for Aldabra Rail eggs in the 2000/2001 breeding season with all data censored at 20 days.

redated; we found no other repeat clutches on Malabar.

Timing of rail reproduction was closely tied to onset of the wet monsoon and concomitant increase in invertebrate densities. Laying of first clutches in the 2000/2001 breeding season on Picard was concentrated around the end of December and early January, although one successful clutch was laid in mid-November, before the monsoon began. Eggs were laid at intervals of 1–4 days, typically every other day.

The incubation period (from last egg to first-hatched chick) was 19–24 days (mean = 21.2 days, n = 5 nests). Individual eggs took 22–24 days from laying to hatching (mean = 22.6 days, mode = 22 days, n = 11 eggs). The hatching interval was 0–3 days, synchrony being the norm, implying that incubation typically starts after clutch completion. Chicks are semi-precocial (*sensu* Starck and Ricklefs 1998); they hatch downy and are able to follow parents from hatching onwards. They can leave the nest within a few hours of hatching and abandoned the nest within 3 days. Eggshells were not found and one female was observed to eat the hatched egg shells. Infertile eggs were abandoned in the nest (n = 2). Newly hatched chicks left the nest for periods in the care of one parent when infertile or late-developing eggs were being incubated. Repeat clutches were timed so that juveniles from the first brood were evicted from the territory before the next clutch hatched (n = 6). Parents adopted one of two caring and provisioning strategies once the nest was abandoned. They either divided the brood between themselves and provisioned young independently, or they left chicks well concealed, foraged alone, and returned to the chicks with food. The latter strategy was only used for downy chicks. Downy chicks often gave a continuous, high-pitched *peep* begging call while following foraging adults. Chicks immediately ran to the nearest dark place when parents gave a danger call. Parents provisioned chicks until they were 6–8 weeks of age and became aggressive towards chicks when they attained full juvenile plumage, at ~8 weeks of age. Aggressive interactions continued until offspring left the natal territory (generally at 8–10 weeks of age).

Two of 12 nests found during incubation failed to produce any chicks. The Kaplan-Meier survival function for eggs (Fig. 3) showed relatively low failure rate due to predation. The overall survival rate was inflated because eggs that were infertile but survived beyond 20 days were not counted as failures in the analysis. Overall, the daily survival rate of eggs was 97.5% and the Mayfield estimate of nest success during incubation was 77.0%. Hatching success was 60.9% (28 of 46 eggs from 15 complete clutches). The 18 eggs that failed did so because of presumed predation (7), breakage (3), and presumed infertility/other causes (8). Only one nest (containing 2 eggs) was entirely depredated: all other predation events involved the loss of single eggs. Chick survival was 57% with 16 of 28 hatchlings surviving to independence. Breeding success on Picard was 1.05 chicks per nesting attempt (n = 17 attempts), although breeding success of repeat clutches following successful first clutches was only 0.75 chicks per nesting attempt (n = 8 attempts, Table 1).

Behavior.—Adult Aldabra Rails used a variety of vocalizations, postures, and displays, mostly in territorial or sexual contexts. Two prominent plumage features, the white throat patch and white undertail coverts, had particular significance in postures and displays. These features contrast strongly with the darker plumage of the rest of the bird and also stand out against the surroundings of the understory.

The *Relaxed Posture* was used when resting, foraging, and walking. When standing, the neck was bent or retracted with the head pointing horizontally or down, hiding the throat patch. The tail was flicked with each step, but the undertail coverts were not fanned. There were no associated vocalizations except during the early breeding period when males mate-guard and both males and females gave the *mpclick* call continuously and partially displayed the undertail coverts. When sleeping, the head and neck were pulled in and the bill held horizontally, at times while the bird stood on one leg.

Aldabra Rails bathed regularly if fresh water was available. Bathing was done in shallow water and the head dipped repeatedly under the water in a bobbing fashion, spilling water over the upper parts on each rise and wetting the underparts on each dip. A wet bird may sun itself with the wings fanned horizontally. There are no records of alternative bathing activities (e.g., dust bathing or bathing in the sea). When preening, the eyes were kept shut. Allopreening was initiated by gently pecking around the head area. It was initiated by males or females and was also targeted at young birds. Allopreening often preceded other pair-bonding behavior such as duetting and copulation.

The *Greeting Display* (Fig. 4A) was usually performed when pairs reunited after foraging apart; they trotted towards each other with necks partially stretched and vertical, displaying their throat patches. Both gave soft, purring calls and occasionally touched bills. Once birds met, contour feathers were slightly raised and undertail coverts fanned, but the white throat patch was concealed by the low head position and retracted neck.

The *Singing Posture* (Fig. 4B) was used by individuals when calling singly and when duetting. Birds often ran towards each other when duetting and stood close. The bill was held slightly below horizontal and the neck stretched and angled forward and upwards. The body was angled slightly upwards and the legs held in a partial crouch. Calls were variable in length; after calling, birds usually adopted the *Relaxed Posture.*

The *Curious Posture* (Fig. 4C) was given when a rail encountered a novel stimulus such as humans and/or their equipment. The context was similar to that of the *Alert Posture*, although the latter was used when a bird's attention was drawn to something further away, such as when territorial intruders were detected. The neck was stretched and held horizontal. The body was also horizontal and the head at times cocked at an angle. The neck was often retracted and extended at a new angle. The legs were at times in a half-crouch, as if ready to flee. The contour feathers were not raised.

The *Alert Posture* was adopted when a bird was in a similar state of arousal as for the *Curious Posture*, but was not restricted to investigating novel stimuli. It is similar to the *Upright Posture*, but the undertail coverts were not displayed. The body was upright with the neck fully or partially stretched and the throat patch partially obscured. The tail pointed down and coverts and contour feathers were not fanned.

The *Territorial Defense Display* (Fig. 4D) was given when a conspecific intruded on a territory or in a boundary dispute. The body was horizontal and the neck pulled in, par-

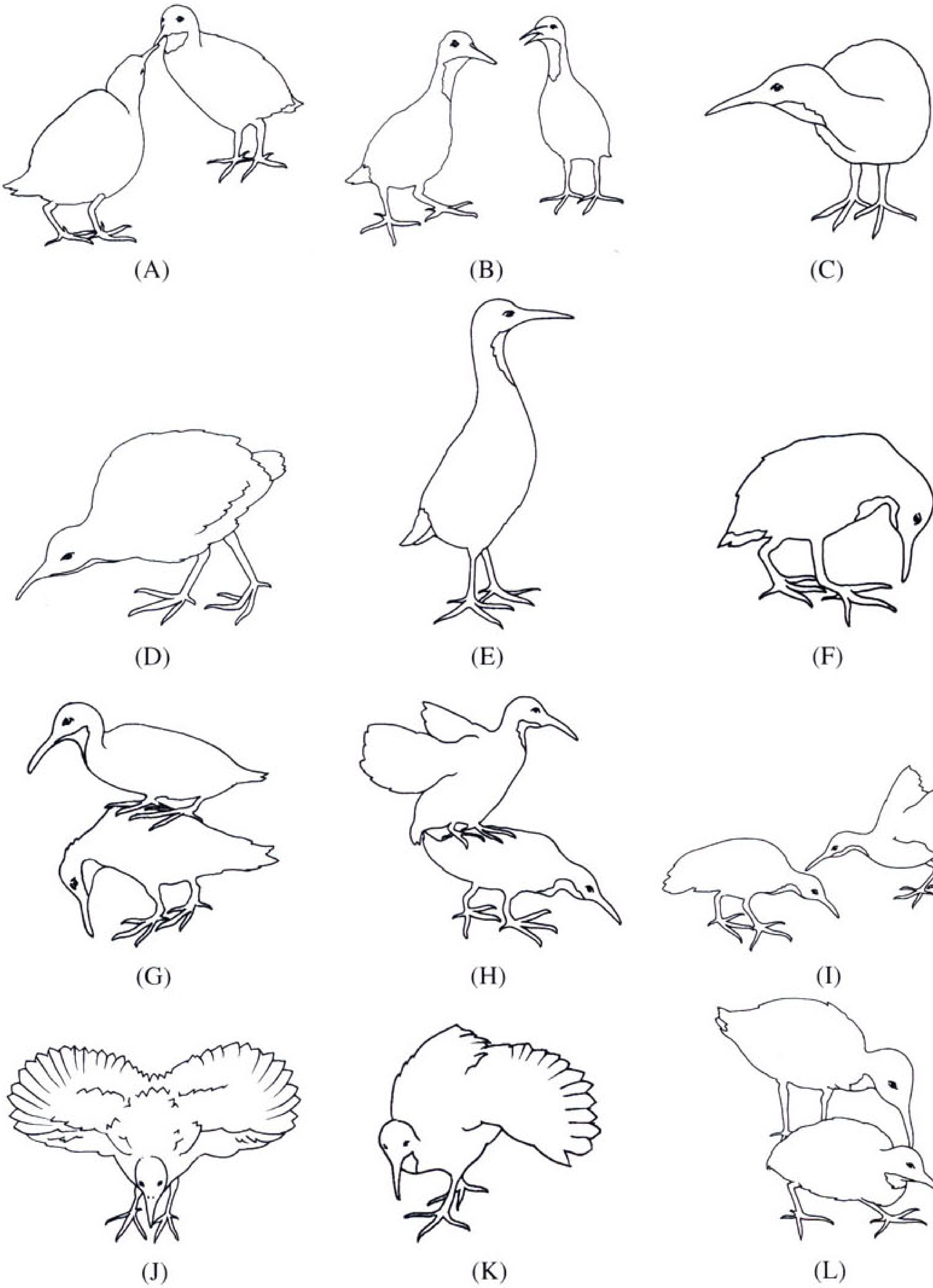

FIG. 4. Postures and displays of the Aldabra Rail based on photographs and field observations. (A) *Greeting Display*, (B) *Singing Posture*, (C) *Curious Posture*, (D) *Territorial Defense Display*, (E) *Upright Posture*, (F) *Invitation Display*, (G) *Mounting*, (H) Coitus, (I) *Post-copulatory Display*, (J) *Full Nest Defense Display*, (K) *Partial Nest Defense Display*, and (L) *Aggressive and Submissive displays.*

tially obscuring the throat patch. The tail was raised, coverts fully fanned, and the contour feathers were all raised. Wings were occasionally held slightly away from the body with primaries partially splayed. Birds approached each other and moved from side to side, flicking the tail with each step. If neither protagonist retreated, they adopted the *Upright Posture* and typically a fight ensued.

The *Upright Posture* (Fig. 4E) was also used in the context of territorial defense. The body was upright and the neck fully extended and held vertically, displaying the throat patch. The tail was held horizontal or pointing slightly downwards with coverts fully fanned. Contour feathers were slightly raised on occasions. It was used during *Aggression Displays* by the aggressor. After the *Upright Posture* was adopted by one or both individuals, if one bird backed down it was usually chased, if not, they fought. Chasing birds held their necks up and out and displayed their throat patches and undertail coverts, whereas fleeing birds kept the tail down, concealing the undertail coverts. Chasing birds flapped their wings to assist in maneuvering. The *Chasing Posture* was also used by adults when evicting their offspring from the natal territory and, in a trespassing situation, against neighbors or their offspring. The pursuing bird pecked the fleeing bird whenever it could reach it.

Birds circled each other as a prelude to fighting or approached head-on in the *Territorial Defense Stance.* They then suddenly adopted the *Upright Posture* (fully displaying their throat patch) and attacked, leaping and kicking each other simultaneously, while flapping their wings vigorously and directing blows with their bills. They either landed on their feet and repeatedly circled and jumped at each other, alternating between the *Upright* and *Territorial Defense Postures*, or they fell to the ground, facing each other while balancing on their tails and wings and kicking vigorously. Fights were violent and occasionally resulted in serious injury or death.

A series of postures was used before, during, and after copulation. The sequence of events appeared to be fixed with the exception of the initiation. Incomplete events may have been due to the presence of observers, but we believe mounting was a pair-bonding activity; when cloacal contact was absent, the behavior is referred to as *Pseudo-copulation. Pseudo-copulation* was frequent in the months before reproduction began and after young had left the natal territory.

Copulation was usually preceded by duetting. It was initiated in one of two ways. Birds adopted the *Approach Posture*, moved towards their mates with the neck stretched vertically, body angled up (but not as much as in the *Upright Posture*), displaying the throat patch and undertail coverts. Alternatively, initiation of the sequence began when a bird faced away from its mate and performed the *Invitation Display* (Fig. 4F). This was present in all copulation sequences observed. A bird in the *Invitation Display* arched its neck and pointed the bill downwards. The body was angled upwards and the bird waddles forward a few paces in a half crouch, slowing quickly to a standstill. The tail was pointed down, the undertail coverts fanned and the wings folded. A responsive mate adopted the *Approach Posture,* walked or trotted towards its mate, and then mounted the inviting bird (Fig. 4G). It then crouched on the latter's back, the body almost horizontal, tarsi touching the other bird's back, the head pointing down at 45°, with wings folded and the undertail coverts fully fanned. The mounted bird then raised its tail while displaying the undertail coverts. The head and neck positions changed repeatedly but were probably related to maintaining balance. The mounting bird then tread on the other bird's back a few times, leaned back, fluttered its wings for stability, and moved its tail under that of the inviting bird's to make cloacal contact, usually for no more than 1–2 sec (Fig. 4H). Normally, the entire copulation sequence was repeated with roles reversed, including reverse mounting. After dismounting, the bird performed the *Post-copulatory Display* (Fig. 4I), walking in a semi-circle around the front of its mate, which remained in the *Invitation Display.* The wings were fanned and vertical, with the leading edge towards the ground. The contour feathers were raised, with the head held low and the neck held the same way as in the *Nest Defense Display.*

Nest Defense Displays (Fig. 3J–K) were directed at any intruder that approached too close to the nest or chicks, except for crabs, which were vigorously pecked. Birds rushed towards the intruder in the *Full Nest Defense*

Display (Fig. 4J) with wings held fully open and vertical, and the leading edge pointing towards the ground. The body was held low and horizontal and the head kept close to the body, facing the intruder while obscuring the throat patch. The undertail coverts were fully fanned. The mantle and back feathers were slightly raised. The displaying bird stopped and walked back and forth ~1 m in front of the intruder. Birds also made rapid attacks with a single, jabbing peck at the intruder. If the intruder didn't advance further, the displaying bird would at times circle the intruder. The intensity of the display decreased quite rapidly and birds adopted the *Partial Nest Defense Display* (Fig. 4K) with both wings partially folded or, more usually, the wing away from the intruder completely folded. This was followed by a *Staring Display* identical to the *Territorial Defense Display* except the contour feathers were completely raised and the displaying bird usually stood still and stared directly at the intruder; the contour feathers were gradually lowered as the display ended. An incubating or brooding bird stayed on the nest until the intruder was within 1 m if a mate was present and displaying. The bird left the nest in the *Full Nest Defense Display* if the intruder came closer, and either charged at the intruder or moved to the side (possibly in an attempt to divert attention from the nest). If an intruder attempted to raid the nest, the incubating bird stood next to or over the nest and attacked the intruder, making powerful, jabbing pecks and giving a loud, piercing squeal that was only given in this context. Birds often followed a retreating intruder, at times in the *Partial Nest Defense Display*. At this ostensibly critical juncture, birds occasionally stopped mid-display to feed; this may have been displacement behavior.

When 'courtship feeding' or provisioning young, a bird with food in its bill approached the intended recipient and adopted the *Provisioning Posture*. The head was pointed vertically downwards so the bill almost touched the ground. The rest of its body was in the *Relaxed Posture*. This posture was maintained until the food item had been taken. If a chick dropped food or struggled to handle it, the adult would pick it up repeatedly, at times breaking the item into smaller pieces. The chick usually approached the adult in this posture from the side and underneath, small chicks even standing under the chest of the adult.

Aggressive and *Submissive Displays* (Fig. 4L) were distinct from the *Territorial Defense Display* and differed from the positions for fighting in that only one bird was aggressive. These displays formed part of intra-pair behavior and were also used when adults evicted young from the natal territory. When a bird performed the *Aggressive Display*, it adopted the *Upright Posture* while approaching another bird. It then stood over the other bird and leaned forward when attacking. The aggressor would also grab the other bird's head or neck in its bill or push the other bird with its chest. The bird being attacked either adopted a *Submissive Posture* or fled. In the *Submissive Posture*, the bird crouched on the ground with its neck retracted and the head pointing down and away from the aggressor, hiding the throat patch. No undertail coverts were visible, the wings were kept folded, and the contour feathers were flattened. We only observed intra-pair aggression arising from direct competition for food outside the breeding season. During the breeding season it appeared to be a pair-bonding behavior, but was also used in competition for food. Where gender of birds in intra-pair aggressive interactions was known, the aggressor was usually male.

DISCUSSION

Aldabra Rails form monogamous pairs that vigorously defend their territories against intruders; both pair bonds and territory boundaries were stable across breeding seasons. Males and females shared duties associated with breeding (e.g., incubation and chick provisioning) and territoriality (e.g., territorial defense). They foraged in all vegetation types on Aldabra but preferred dense mixed scrub (Penny and Diamond 1971, Wanless 2002). They were seldom encountered in monospecific stands of *Casuarina equisetifolia*, possibly reflecting a paucity of understory cover or low invertebrate prey densities (Spaull 1979). They regularly foraged in mangrove (*Rhizophora* sp.) swamps, but vacated these at high tide (Penny and Diamond 1971, this study). In addition to terrestrial arthropods, which dominate the diet, they also eat berries, flower petals, intertidal invertebrates, organic jetsam on beaches, turtle and tortoise eggs and hatchlings, skinks, geckos, crabs, carrion, and kitchen scraps (Penny and Diamond 1971, Frith 1977, Huxley 1982, this study). Neither this study nor Huxley's (1982) quantified the diet of Aldabra Rails. This was due to the difficulties of observing birds in dense vegetation without disrupting their feeding. Slow-motion replay of video recordings is probably the only way to gather reliable data on feeding ecology.

A significant finding of this study is that gender of Aldabra Rails cannot be reliably ascertained in the field. We incorrectly identified gender of 11 birds that were in the hand at the time and could be closely examined. This casts doubt over interpretations of Aldabra Rail biology and behavior from earlier studies (e.g., Penny and Diamond 1971, Huxley 1982). It also led to the discovery of reverse mounting in the species.

A second finding that refutes published information about Aldabra Rails relates to their territoriality. Penny and Diamond (1971) argued that territories are not necessarily contiguous, but conform to a 'neighborhood' system, where core territories are defended but communal foraging areas exist. Neither Huxley (1982) nor we found any evidence to support this assertion.

Huxley (1979) described a mutualistic relationship between Aldabra Rails and Aldabra giant tortoises (*Dipsochelys dussumieri*). The rails reportedly glean flies, dead skin or ectoparasites from tortoises, which in turn assist by adopting a distinctive posture, exposing the full surface of skin to be gleaned. Neither we nor anyone else with whom we have worked or consulted has witnessed this interaction. On the contrary, Aldabra Rails regularly foraged less than a meter from giant tortoises and neither species showed the slightest interest in the other.

A recent text on the Aldabra Rail (e.g., Sinclair and Langrand 1998) treated it as a distinct species from the White-throated Rail of Madagascar. A taxonomic review based on genetics and vocalizations is presently underway, but a greater understanding of the Aldabra Rail's biology is necessary in understanding its evolution, distinctiveness, conservation status, and threats to its persistence on Aldabra. In addition, there are consistent differences in plumage coloration between birds from Île aux Cèdres versus Malabar and Polymnie islands that merit closer investigation.

The reintroduced population (on Picard) produced clutches of up to four eggs, in contrast to the limited evidence of three-egg clutches being the maximum on Malabar. This suggests the species' maximum clutch size is four. We failed to find second clutches following successful first clutches on Malabar, but at least six pairs on Picard attempted double-brooding. The Aldabra Rail's response to good breeding conditions appears to be to increase reproductive effort by increasing clutch size and clutch frequency. Huxley (1982) reported two repeat clutches from Malabar pairs (no total sample size given). In general, it is likely that replacement clutches will be laid but repeat clutches are expected to be quite rare.

There are three points of particular interest regarding reproductive displays of the rails. One, termed *pseudo-copulation*, involves mounting but excludes cloacal contact. We interpret this as a pair-bonding activity. The second is reverse mounting (where the female mounts the male). This behavior has been reported from a diversity of bird species (James 1983), including rallids (e.g., Anderson 1975, Brooke 1992). Reverse mounting is known to be a regular component of pair bonding/sexual behavior in relatively few bird species (James 1983, Nuechterlein and Storer 1989). Last, the *Post-copulatory Display* was described by Frith (1977) who conjectured that it was restricted to extra-pair copulations—this is not the case.

Aldabra has five species that are potential nest predators: the terrestrial Robber Crab (*Birgus latro*), Malagasy Kestrel (*Falco newtoni*), Malagasy Coucal (*Centropus toulou*), Pied Crow (*Corvus albus*), and black rat (*Rattus rattus*), the latter being an introduced species. The loss of seven eggs (5 of which were individual losses from successful clutches) and 12 of 28 chicks suggests that nest predators are successful in raiding Aldabra Rail nests and in preying on nestlings. However, Aldabra Rails have strong nest and chick defense instincts. First, they do not flush from the nest in the same way as species that have high adult mortality rates at the nest (cf. Conway and Martin 2000, Lloyd 2004). Second, the hiding behavior of chicks in response to the danger call from parents is strong. Furthermore, no adult Aldabra Rail has ever been reported to be attacked by predators. These data lend support to the hypothesis that eggs and chicks are at risk of predation, but adults are not, or at least much less so, given the absence of other (introduced) predators. We posit that Aldabra Rails have evolved on Aldabra in the absence of predators of adults and lack appropriate behaviors. The *Nest Defense* displays described would be entirely inappropriate for a predator capable of taking adult Aldabra Rails.

The present-day absence of significant predators of adult Aldabra Rails is fortuitous. They are not at risk from black rats (Penny and Diamond 1971; Frith 1977; Huxley 1982; Wanless 2002, 2003b). Rats typically retreat in the face of aggression from Aldabra Rails, which are capable of killing them (Wanless 2003b). The ranges of Aldabra Rails and feral domestic cats (*Felis catus*) do not overlap on Aldabra and cats are thought to be largely responsible for the local extinction of Aldabra Rails on Grande Terre and Picard islands (Wanless 2002). However, local extinctions happened before many interactions were recorded and there are only two records of Aldabra Rails interacting with cats (Huxley 1982, Hambler et al. 1993). In both instances, Aldabra Rails adopted a *Nest* or *Territory Defense Posture* rather than flee. This implies that Aldabra Rails do not have an appropriate (i.e., fleeing) response to cats, and do not treat them as potential predators. The presence of the Norway rat (*Rattus norvegicus*) elsewhere in the Seychelles is a source of concern, as it is bigger and more aggressive than the black rat, and its impacts on insular avifauna are much greater (Towns et al. 2006). We predict that inappropriate responses of Aldabra Rails to cats (and to humans close to their nests) are likely to be similarly maladaptive for other novel predators. Dispersal of cats, Norway rats or other mammalian predators to any of the four islands where the Aldabra Rail now occurs will pose a significant threat to the survival of the species. Quarantine/bio-security procedures that minimize risk of further colonizations should be a priority and put in place for all visits to Aldabra.

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