

The large *Porphyrio madagascariensis* (African Swamphehen) and the smaller but similarly colored *P. alleni* are widespread and often numerous in herbaceous freshwater marshes dominated by reeds (*Phragmites*), sedges (Cyperaceae), and bullrushes (*Typha*), and on lakeshores of the western lowlands; they are present but scarcer in the east below 800 m elevation. *Porphyrio madagascariensis*, despite its scientific name, also occurs in Egypt and sub-Saharan Africa. *Porphyrio alleni* is otherwise found only in Africa, although its movements, as discussed above, deserve much greater study. The elephantine trumpeting of the bold and conspicuous *P. madagascariensis* can be a characteristic sound of Malagasy wetlands, while *P. alleni* is far less obtrusive, foraging more often on floating aquatic plants with discreet and inconspicuous movements, in keeping with general shyness.

Gallinula chloropus (Common Moorhen) is an almost cosmopolitan species, but the birds on Madagascar (race *G. c. pyrrorhoa*)

are distinctive, having buff undertail coverts (not white as in all other races); whatever their color, these form a striking feature used in signaling conspecifics, as the birds flick their tails up frequently. Similar birds occur on Mauritius, La Réunion, and the Comoros. On Madagascar they are widespread, but generally not abundant, in a wide range of wetland habitats, primarily inland fresh waters with stretches of open water. Larger open-water habitats may be used by *Fulica cristata* (Red-knobbed Coot), another African and Malagasy species, but in this case without known geographic variation. It has been widely recorded on Madagascar up to 1500 m but is very localized, and absent from many localities that appear suitable based on habitats used in Africa; the largest numbers have been recorded in the west and south.

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CHARADRIIDAE: CHARADRIUS, PLOVERS

S. Zefania and T. Székely

Madagascar has four resident breeding species of *Charadrius* plovers: *C. pecuarius* (Kittlitz's Plover), *C. thoracicus* (Madagascar Plover), *C. marginatus* (White-fronted Plover), and *C. tricollaris* (Three-banded Plover). After the pioneering observations of Otto Appert (Appert 1971), over the past decade the first three species have been the subject of focused fieldwork in the southwest (Andavadoaka in the Mikea region and Tsimanampesotse south of Anakao) and northwest (Namakia and Marambitsy Bays), as they inhabit many of the same coastal sites and habitats. This information is reviewed herein; *C. tricollaris* is ecologically rather distinct, and a short account based largely on other studies is added for completeness.

CHARADRIUS PECUARIUS, KITTLITZ'S PLOVER, VOROMBATO

Charadrius pecuarius is common and distributed broadly across much of the African continent and on Madagascar (Figure 13.20a). On the island, it can be found in a variety of aquatic habitats (Zefania and Székely 2013a), especially open wetland fringe habitats such as salt pans, along rivers, areas with short grass, rice fields, and mudflats. This species usually occurs in natural wetlands, although it can tolerate human-related activities such as salt extraction and livestock grazing.

Plumage and Body Size

Although *C. pecuarius* was previously considered sexually monomorphic (Zefania et al. 2010), the authors' own closer observations of many breeding birds have revealed slight sexual dimorphism in

the black-and-white head markings and brightness of the belly color, these being, respectively, more sharply marked and rufous brown in females (Zefania and Székely 2013a, with further details from the authors' unpublished data). Plumage of the young is similar to that of adults, but without black bars on the head and no brown or rufous on the breast or belly. Downy chicks are generally brown with some white on the underparts.

In a field study involving measurements of 64 *C. pecuarius* individuals (30 male and 34 female, sexed using molecular techniques), no sexual size dimorphism in external measurements was found (Zefania et al. 2010; Zefania and Székely 2013a). The mean body mass of adult females was 34.4 g (range 27.3–42.0 g, $n = 545$) and of adult males was 33.1 g (range 27.8–40.6 g, $n = 658$); mean bill length of adult females was 16.5 mm (range 12.6–19.9 mm, $n = 509$) and of adult males was 16.5 mm (range 14.0–20.0 mm, $n = 614$); and mean tarsus length of adult females was 31.4 mm (range 27.2–35.5 mm, $n = 529$) and of adult males was 31.7 mm (range 26.5–37.0 mm, $n = 645$).

Distribution

On Madagascar, *C. pecuarius* occurs mainly in coastal and inland lowland areas but has been recorded up to 1400 m (Zefania and Székely 2013a). It is more common along the western and southern coasts than in other areas of the island. Open salt marsh habitats of the west constitute an important breeding habitat. At a local scale, its distribution can be influenced by rainfall, which provides standing water and presumably increased prey abundance. This species often nests close to the water's edge. The largest breeding populations found to date have been near Andavadoaka (2010 to 2019),

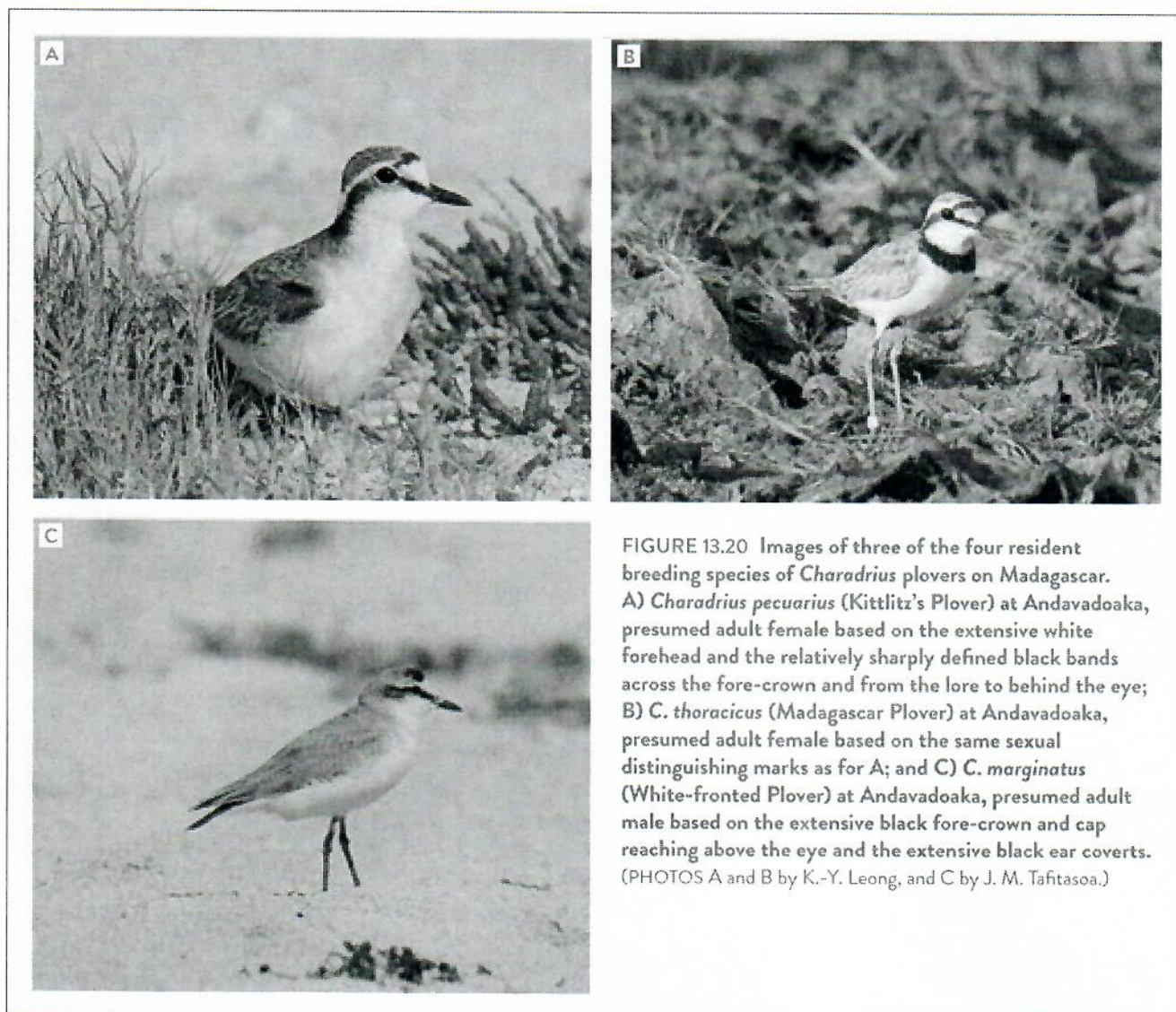


FIGURE 13.20 Images of three of the four resident breeding species of *Charadrius* plovers on Madagascar. A) *Charadrius pecuarius* (Kittlitz's Plover) at Andavadoaka, presumed adult female based on the extensive white forehead and the relatively sharply defined black bands across the fore-crown and from the lore to behind the eye; B) *C. thoracicus* (Madagascar Plover) at Andavadoaka, presumed adult female based on the same sexual distinguishing marks as for A; and C) *C. marginatus* (White-fronted Plover) at Andavadoaka, presumed adult male based on the extensive black fore-crown and cap reaching above the eye and the extensive black ear coverts. (PHOTOS A and B by K.-Y. Leong, and C by J. M. Taftasoa.)

with a minimum of 100 to 300 individuals per breeding season, and Lake Tsimanampesotse (2004 to 2012), with a minimum of 50 to 70 individuals per breeding season (S. Zefania et al., unpublished data).

Food

No information on the diet of this species is available from Madagascar, but elsewhere in its range it is an animalivore, gleaning insects and other invertebrates off the ground in salt marshes, mudflats, and open grasslands (Zefania and Székely 2013a). On low-tide mudflats they probably consume a range of small invertebrates.

Breeding Ecology

Breeding period and laying dates: Breeding appears to peak during the rainy season, the timing of which varies between sites. In drought years, breeding activities are notably reduced or even

absent. The number of nests per site is positively correlated with the amount of rainfall. For example, near Andavadoaka, breeding was recorded from February to June and from October to November (and egg laying noted in February, March, April, October, and November), with a wet season peak in March to April; at Tsimanampesotse the birds bred from January to July (egg laying in February to April); but around Namakia and Marambitsy Bay (Mahavavy Kinkony protected area) they did so from September to October. Evidently, breeding is not synchronized across the range, as is also shown by a nest with eggs in November, and a flightless chick in February, both in the lower Mangoky region (Appert 1971). The period between the first and second egg-laying dates was 2–4 days (mean 3.0 days, $n = 17$ nests).

Nest and eggs: The nest is a small scrape dug into dry soil and surrounded by vegetation and other materials (Zefania and Székely 2013a). When the incubating parent leaves the nest, it typically covers the eggs with loose soil by quick movements of its feet,

presumably to protect the eggs from predators and solar radiation (S. Zefania and T. Székely, unpublished data).

Mean egg length at Andavadoaka was 30.8 mm (range 27.3–34.6 mm, $n = 1028$) and width 21.6 mm (range 20.0–24.8 mm, $n = 1597$). Clutch size was typically two eggs (Zefania and Székely 2013a), with a mean of 1.9 ± 0.36 ($n = 1019$ nests). Out of 1019 examined nests, 151 had one egg and 868 had two eggs. One-egg clutches may be the result of partial predation.

Incubation and chick-rearing periods: Incubation usually commenced some days after the second egg laying and lasted between 22 and 28 days (mean 25 ± 2 days, $n = 17$ nests). Chick rearing lasted approximately four weeks.

Nesting Success and Survival of Young and Adults

In general, this species has low nesting success, and the main cause of nest failure is predation. For instance, at Andavadoaka, out of 883 nests followed, 27.5% produced at least one chick, and, based on inference or direct observation, the 72.5% losses were caused by predation (58.7%), abandonment (11.8%), flooding (0.1%), trampling (1.5%), or infertile eggs (0.5%) (S. Zefania and T. Székely, unpublished data). Predation was assumed to have occurred if the eggs disappeared before the expected hatching date or the banded parents were found without chicks on or just after the expected hatching date. Hence, high nest predation appears to be the limiting aspect in breeding success.

Chick survival is low, and out of 194 chicks monitored at Andavadoaka, 5.7% survived to near the fledgling stage at about 25 days of age, or a body mass of 20 g or more. Survival rates varied among sites and breeding seasons. For adults, maximum known survival is nine years, based on one adult female first captured and marked at Andavadoaka in 2009 and recaptured in 2017 (S. Zefania and T. Székely, unpublished data). Nest and chick predators include *Corvus albus* (Pied Crow), *Felis silvestris* (Wild Cat), and *Falco newtoni* (Madagascar Kestrel).

Behavioral Ecology

Courtship and mating system: The mating system of this species can be pieced together from different observations and summarized as largely polygamous with male-only parental care (Parra 2014; Maher et al. 2017). Male adults provide brood care more often than females, which would imply polygamy (Eberhart-Phillips et al. 2018). Based on molecular testing, not a single brood out of 15 tested showed evidence of extra-pair parentage (Maher et al. 2017). There was no case of more than two adults being associated with a given nest. Changes of partners were found interannually: out of 26 pairs monitored at Andavadoaka, 62% changed partner once or twice between years and the remaining pairs did not change.

Nest and brood care: There is a cycle followed by the two attending adults. Based on passive integrated transponder (PIT) tags placed at five nests (four in 2015 and one in 2019), females incubated mostly during the day and males during the night, particularly from 22h until dawn (S. Zefania and T. Székely, unpublished data), similar to other plover species (Vincze et al. 2013). In some cases,

the male took over from the female during the hot period of the day between 9h and 15h. In general, incubation was particularly intense between 10h and 15h (Vincze et al. 2017) to shade the eggs, and during the cold period, between 16h and 9h, to keep the eggs warm. Recorded images from 40 nests showed that at the beginning of the nesting period the female of the pair spent more time incubating (80%) than the male (20%); female participation then decreased progressively during the incubating period as compared to that of the male, which increased until the eggs hatched.

Male-biased brood care is common in *C. pecuarius* (Eberhart-Phillips et al. 2018). Broods in this species, based on over 705 followed pairs and their broods at Andavadoaka, were cared for by the male in 83.1% of pairs/broods, and by the female in the rest (S. Zefania and T. Székely, unpublished data); biparental care of chicks has not been observed in this species (Parra 2014).

Movements and Dispersal

Marked *C. pecuarius* individuals were found to make local movements of a maximum of 15 km between study sites and years. However, this species almost certainly disperses over greater distances; the Madagascar population shows homogeneous genetic structure (Eberhart-Phillips et al. 2015; J. Jackson et al. 2017), which would support broad dispersal patterns and facilitate gene flow through extensive social interactions (Cunningham et al. 2018). During the nonbreeding period this species occurs in groups, which forage in various wetland habitats.

Threats and Conservation

Charadrius pecuarius has a wide range and large population and uses a variety of habitats; on the IUCN Red List it is considered Least Concern (BirdLife International 2020a). Low breeding success appears to be an important factor limiting its population dynamics on Madagascar. This species shows a low prevalence of *Plasmodium* infection, with one (female) of 58 examined individuals infected by this blood parasite (Martínez-de la Puente et al. 2017).

CHARADRIUS THORACICUS, MADAGASCAR PLOVER, VOROMBATO

This species is endemic to Madagascar and its distribution is limited to the coastal area of the west (P. Long et al. 2008; Zefania et al. 2008) (Figure 13.20b). It breeds mainly in natural wetland habitats, ranging from open salt marshes to areas of short grassland or sandy beaches with some vegetation. It can tolerate some human activities such as fishing and salt extraction and often occurs close to footpaths.

Plumage and Body Size

Like *C. pecuarius*, breeding *C. thoracicus* was previously considered sexually monomorphic in plumage coloration (Zefania et al. 2010; Zefania and Székely 2013b), but we have subsequently found sexual differences, with the female showing sharper definition of the black-and-white crown and forehead patterns (S. Zefania et al., unpublished

data). Plumage of young birds lacks the black head band of adults, and the breast band is present but grayish brown. Downy chicks are generally pale brown on the back and white on the underside.

This species shows slight but significant (not discernible in the field; hence “cryptic”) sexual size dimorphism in external measurements, females being heavier and longer winged than males, whereas males have longer tarsi (Zefania et al. 2010; Zefania and Székely 2013b). For birds sexed using molecular techniques, the mean body mass of adult females was 37.5 g (range 28.0–44.7 g, $n = 349$) and of adult males was 36.1 g (range 29.8–42.2 g, $n = 287$); mean bill length of adult females was 16.6 mm (range 15.0–19.2 mm, $n = 276$) and of adult males was 16.4 mm (range 14.5–19.3 mm, $n = 238$); mean tarsus length of adult females was 32.8 mm (range 28.9–38.4 mm, $n = 346$) and of adult males was 33.1 mm (range 29.5–36.5 mm, $n = 282$); and mean wing length of adult females was 109.5 mm (range 100–119 mm, $n = 344$) and of adult males was 108.5 mm (range 102–114 mm, $n = 282$).

Distribution, Habitat, and Population

Charadrius thoracicus is endemic to Madagascar and restricted largely to the western and southern coastal band, from just north of Mahajanga to the region around Tolagnaro. There are older records of this species in the eastern portion of the island and in the Central Highlands, the latter being particularly unusual and perhaps best explained by cyclone-caused vagrancy (Zefania and Székely 2013b). It occurs in sympatry with *C. pecuarius* in both foraging and breeding sites, particularly open salt marshes, as well as areas of open short grassland and sandy beach. As with *C. pecuarius*, the local distribution can shift as a function of rainfall patterns and associated distribution of water.

Breeding takes place in open grasslands and dry mudflats around mangroves and alkaline lakes, only rarely on sandy soil (Zefania and Székely 2013b), and generally close to the water's edge. The largest breeding populations known are near Andavadoaka (monitored between 2010 and 2019), with a minimum of 100 to 150 individuals per breeding season, and Lake Tsimanampesotse (2004 to 2012), with a minimum of 50 to 100 individuals per breeding season (S. Zefania et al., unpublished data). Based on predictive habitat modeling and population density estimation, P. Long et al. (2008) proposed a global population estimate of 3100 ± 396 (SE) individuals.

Food

No detailed data are available, but the species is presumed to be an animalivore, gleaning insects and other invertebrates off the ground in salt marshes, mudflats, and open grasslands (Zefania and Székely 2013b). On mudflats exposed at low tide, they probably consume a range of small invertebrates.

Breeding Ecology

Breeding period and laying dates: Breeding often but not always takes place during the rainy season and is often correlated with the start of rains (Zefania and Székely 2013b), but there is much inter-site variation across the island. Near Andavadoaka, birds breed during two periods from February to June, with a peak from March

to April (recorded egg-laying dates from February to May) but also from October to December; at Tsimanampesotse, they breed from October to June (recorded egg-laying dates from December to April); and in the northwest around Marambitsy Bay, from April to May and November to December (with egg laying also recorded in August). The period between the first and second egg-laying dates was 3–4 days at four nests (mean 3.5 days). During the nonbreeding period, this species occurs in groups, foraging together in wetland habitats, often with other *Charadrius* species.

Nest and eggs: The nest is a small scrape dug into dry soil with both vegetation and other materials (Zefania and Székely 2013b). In a similar way to *C. pecuarius*, the incubating parent covers the nest when leaving it by movements of its feet (S. Zefania and T. Székely, unpublished data).

Mean egg length at Andavadoaka was 32.2 mm (range 27.7–35.6 mm, $n = 927$) and width 22.9 mm (range 20.2–25.6 mm, $n = 925$). From our sample of 895 nests, the modal clutch size was two eggs (Zefania and Székely 2013b), with a mean of 1.9 ± 0.36 ; 134 had one egg and 761 had two eggs. One-egg clutches might be the result of partial predation.

Incubation and chick-rearing periods: Egg incubation usually commenced some days after the second egg was laid, and the incubation period was between 28 and 32 days (mean 29 ± 1 days, $n = 14$ nests). The chick-rearing period was approximately four weeks.

Nesting Success and Survival of Young and Adults

Charadrius thoracicus has relatively low nesting success, and the main cause of nest failure is predation. For instance, at Tsimanampesotse, out of 270 nests followed, only 37.0% produced at least one chick, and based on inference or direct observation, the remaining 63.9% were lost to predation (37.4%), abandoned (10.7%), flooded (11.5%), trampled (1.3%), or had infertile eggs (3.0%) (S. Zefania and T. Székely, unpublished data). Chick survival is also low, and out of 390 chicks monitored at Andavadoaka, only 18.7% survived to near the fledgling stage at about 20 days of age or a body mass of 23.7 g or greater. There were slight differences in the survival rate among sites and breeding seasons. For adults, apparent annual survival rates were 80% determined using data from 176 banded adults from 2004 and 2007. Maximum known survival is 11 years, based on an adult male captured and marked at Andavadoaka for the first time in 2009 and recaptured 10 years later (S. Zefania and T. Székely, unpublished data). Nest and chick predators are probably similar to those of *C. pecuarius*.

Behavioral Ecology

Courtship and mating system: Few details are known about the mating system of this species, but it is considered monogamous with biparental care (Zefania et al. 2008; Maher et al. 2017). Monogamy is suggested by both individuals of a pair providing nest and brood care (Eberhart-Phillips et al. 2018). Further, based on molecular testing, extra-pair paternity is rare, as not one out of 12 broods analyzed had young sired by another male (Maher et al. 2017). No example of more than two adults associated with a nest

was found. Changes of partners were found interannually: out of 72 pairs monitored at Andavadoaka, 56% changed partner once or twice between years.

Nest and brood care: Both adults take part in nest care, with females taking charge during the day (6h to 21h) and males from after dark to dawn (21h to 6h) (Vincze et al. 2013; S. Zefania and T. Székely, unpublished data). In some cases, the male took over during the hot period of the day between 9h and 15h. The function of nest incubation appeared to be to shade the eggs during the hottest period, mainly between 10h and 15h (Vincze et al. 2017), and to keep them warm during the cold period, between 16h and 9h. Based on recorded images from 18 nests, at the beginning of the nesting period the female spent more time incubating (80%) than the male (20%), but her participation decreased progressively as the male's increased, to 60% by the female and 40% by the male at the end of the incubation period.

Biparental brood care is common in *C. thoracicus* (Zefania and Székely 2013b; Eberhart-Philips et al. 2018): at Andavadoaka, in 83% of families ($n = 464$ nests), broods were cared for by both adults, while at Tsimanampesotse the corresponding figure was 69% ($n = 363$ nests) (S. Zefania and T. Székely, unpublished data). Male-only brood attendance increased with chick age (Parra 2014).

Movement and Dispersal

Adults seem to be largely sedentary. Marked *C. thoracicus* showed local movements of a maximum of 15 km between study sites and years. For juveniles, there is evidence of wider dispersal: an individual banded at Tsimanampesotse in March 2007 was found four months later at Ifaty, a distance of 100 km; another banded at Andavadoaka in April 2019 was located four months later near Morondava, a distance of about 250 km. Because adults are sedentary, their populations are poorly interconnected, resulting in a strong or heterogeneous population structure (Eberhart-Philips et al. 2015; J. Jackson et al. 2017).

Threats and Conservation

Charadrius thoracicus is classified as Vulnerable on the IUCN Red List (BirdLife International 2020a) based on its localized population, which is thought to be undergoing a continuous decline owing to pressures on its wetland habitats (see also Young et al., pp. 1627–36). Low breeding success appears to be the main population-limiting factor for this endemic species. It showed no evidence of *Plasmodium* infection in the 55 examined individuals (Martínez-de la Puente et al. 2017). A portion of the habitats and sites this species uses for feeding and breeding occur in the current protected area system, but additional inclusion of salt marshes in the network is still recommended.

CHARADRIUS MARGINATUS, WHITE-FRONTED PLOVER, VOROMBATO

Charadrius marginatus occurs (as three subspecies) in many coastal areas of Africa, as well as patchily inland; it is also found quite

widely on Madagascar (*C. m. tenellus*), but as in Africa the main breeding zone is along the coast (Zefania and Székely 2013c). There are also observations of this species from Mayotte in the Comoros, but no evidence of breeding.

Plumage and Body Size

Breeding *C. marginatus* was thought to be sexually monomorphic (Zefania and Székely 2013c), but as with the previous two species, closer investigation has shown that the sexes can be differentiated based on plumage, with differences in crown, nape, and forehead patterns, as well as pigmentation patterns of the underside (Figure 13.20c). The plumage of the young differs from that of the adults in the poorly defined black band on the forehead and other markings on the head, subdued coloration on the nape, and white underside. Downy chicks generally have very pale plumage compared to congeners.

This species also shows low-level but significant (i.e., “cryptic”) sexual size dimorphism in external measurements, females being slightly longer winged than males (Zefania et al. 2010; Zefania and Székely 2013c). For birds sexed using molecular techniques, the mean body mass of adult females was 37.1 g (range 30.5–42.5 g, $n = 252$) and of adult males was 36.0 g (range 26.5–45.5 g, $n = 209$); mean bill length of adult females was 14.9 mm (range 12.4–17.3 mm, $n = 218$) and of adult males was 15.0 mm (range 13.4–17.8 mm, $n = 185$); mean tarsus length of adult females was 26.3 mm (range 22.8–31.5 mm, $n = 240$) and of adult males was 26.7 mm (range 24.2–31.0 mm, $n = 193$); mean wing length of adult females was 105.6 mm (range 98–113 mm, $n = 251$) and of adult males was 105.3 (range 100–114 mm, $n = 209$).

Distribution and Habitat

On Madagascar, this species occurs mainly along the western and southern coastal zone, from Analalava to Tolagnaro (Zefania and Székely 2013c). The principal utilized habitats are open wetlands, including salt pans, sandy beaches, mudflats at low tide, and salt marshes, where it occurs in sympatry with *C. pecuarius* and *C. thoracicus*. Inland, most records are on wide, sandy rivers (Appert 1971). It usually occurs in natural wetland habitats but can tolerate some human activities such as salt extraction and cattle grazing.

The local distribution of *C. marginatus* can shift as a function of rainfall patterns and the associated amount of water, particularly in open salt marsh habitat. The breeding zones appear to be broadly distributed along the west coast but tend to be concentrated in salt marshes close to the water's edge. The largest breeding populations known are near Andavadoaka (monitored between 2010 and 2019), with a minimum of 50 to 100 individuals per breeding season, and Lake Tsimanampesotse (2004 to 2012), with a minimum of 30 to 50 individuals per breeding season (S. Zefania et al., unpublished data).

Food

A few data are available from Madagascar, including four stomachs containing marine crustaceans as well as fine stones (Goodman et al. 1997a). Field observations confirm an animalivorous diet, glean-ing insects and other invertebrates, including crabs and other

crustaceans, from the ground in salt marshes, mudflats, and open grasslands (Zefania and Székely 2013c).

Breeding Ecology

Breeding period and laying dates: The breeding period in this species seems not to be highly seasonal; breeding takes place in both the rainy and dry periods and spans all months of the year. For example, near Andavadoaka nesting activities have been documented from February to November, with a peak between March and May (observed egg-laying dates recorded from February to May, and in November); at Tsimanampesotse breeding is from January to May (observed egg-laying dates recorded from January to April); and around Namakia and Marambitsy Bays from April to December. The time between the first and second egg laying was 2–5 days at three nests (mean 3.0 days) and between the second and third egg was 1–5 days at five nests (mean 3.0 days).

Nest and eggs: The nest is a small scrape dug into dry soil without cover or at most a few stones or seashell fragments (Zefania and Székely 2013c); unlike with *C. pecuarius* and *C. thoracicus*, when the incubating parent leaves the nest, it typically does not cover the eggs (S. Zefania and T. Székely, unpublished data).

Mean egg length at Andavadoaka was 30.7 mm (range 24.4–35.8 mm, $n = 1377$) and width 21.9 mm (range 19.0–24.9 mm, $n = 1373$). Modal clutch size was two eggs (Zefania and Székely 2013c), with a mean of 1.99 ± 0.61 ($n = 832$ nests). Out of 832 nests, 156 had one egg, 524 had two eggs, and 151 had three eggs; of the three species studied, only *C. marginatus* had some three-egg clutches. One-egg clutches might be the result of partial predation.

Incubation and chick-rearing period: Egg incubation usually commenced some days after the laying of the last egg in the clutch, and the incubation period was between 22 and 30 days (mean 27 ± 4 days, $n = 6$ nests). The chick-rearing period lasted approximately four weeks.

Nesting Success and Survival of Young and Adults

Like its relatives, *C. marginatus* has low nesting success, and the main cause of nest failure is predation. For instance, at Andavadoaka, out of 373 nests followed, 28.7% produced at least one chick; the rest were lost to predation (61.4%), abandoned (5.9%), flooded (2.1%), trampled (1.9%), or had infertile eggs (0.2%) (S. Zefania and T. Székely, unpublished data).

Chick survival is also low: out of 108 chicks monitored at Andavadoaka, 33.3% survived to near the fledgling stage at about 20 days of age or a body mass greater than 21 g; 8.3% of chicks reached the age of 25 days. There were differences in survival rate between sites and breeding seasons. Maximum known survival is 11 years, based on an adult male captured and marked at Andavadoaka for the first time in 2009 and recaptured in 2019 (S. Zefania and T. Székely, unpublished data).

Behavioral Ecology

Courtship and mating system: The mating system of *C. marginatus* can be pieced together from different observations and summarized

as monogamous and dominated by biparental nest and brood care (Parra 2014; Eberhart-Phillips et al. 2018). Based on molecular analysis, no evidence of extra-pair paternity was detected in 10 tested broods (Maher et al. 2017). No case of more than two adults associated with a nest was found. However, interannual changes of partners were found: out of 41 pairs monitored at Andavadoaka, 85% changed partner once or twice between years. During the non-breeding period this species occurs in groups, sometimes with other *Charadrius* species, particularly *C. pecuarius* and *C. thoracicus*.

Nest and brood care: Incubation was investigated using PIT tags at Andavadoaka at six nests (two in 2015 and four in 2019): females incubated mostly during the day and males during the night (S. Zefania and T. Székely, unpublished data), particularly from 22h until dawn. In some cases, the male took over from the female during the hot period of the day between 9h and 15h. Nest incubation was most constant during the hot period (Vincze et al. 2017), between 10h and 15h, to shade the eggs, and during the cold period, between 16h to 9h, to keep the eggs warm. Recorded images from 40 nests indicate that early in the incubation period the female spent more time on the nest (60%) than the male (40%), but female participation increased slightly to 65% toward the later stages of the incubation period.

Based on over 545 followed broods at Andavadoaka, both parents cared for broods in 70.1% of cases, whereas at Tsimanampesotse this figure, based on 17 followed broods, was 58.8% (S. Zefania and T. Székely, unpublished data).

Movement and Dispersal

Records of local dispersal based on banded *C. marginatus* showed a maximal distance traveled of 15 km between study sites and years. Study of local dispersal in this species at Andavadoaka based on experimentally removed mates (Parra et al. 2014) found spatially discrete and less interconnected populations than in *C. pecuarius* on the breeding and feeding grounds (Cunningham et al. 2018). Genetic comparisons between *C. marginatus* populations showed little phylogeographic structure (Eberhart-Phillips et al. 2015; J. Jackson et al. 2017), suggesting considerable dispersal and mixing.

Threats and Conservation

Charadrius marginatus has a large range and population and uses a variety of habitats; on the IUCN Red List it is considered Least Concern (BirdLife International 2020a). The Madagascar population, if considered separately, does not appear to be at great risk for the same reasons. Low breeding success appears to be an important population-limiting factor for this population. It shows a low prevalence of *Plasmodium* infection, with only one (female) of 55 birds examined infected (Martínez-de la Puente et al. 2017).

OTHER CHARADRIUS SPECIES ON MADAGASCAR

Charadrius tricollaris (Three-banded Plover, *vorombato* or *mondit-*ra**) occurs across much of sub-Saharan Africa and Madagascar but

is associated mainly with inland freshwater wetlands, particularly margins of streams and rivers, muddy ponds in open country, wet rice fields, and artificial lakes; it is not normally found on open coastlines but does use saline habitat at the edges of salt marshes, estuaries, or brackish inland lakes. The distinctive endemic race *C. t. bifrontatus* is widespread on Madagascar, although habitat for it is limited in the dry south and southwest, and it is largely absent from the Central Highlands. The species has not been studied in detail on Madagascar but behaviorally appears to be a typical small *Charadrius* (Appert 1971; Zefania and Székely 2013d).

Three more *Charadrius* species visit Madagascar's coastal wetlands as migrants from the Palearctic region: *C. hiaticula* (Common Ringed-plover); *C. leschenaultii* (Greater Sand-plover); and *C. mongolus* (Lesser Sand-plover) (see Young et al., pp. 1627–36). The latter two are difficult to distinguish, making their status somewhat uncertain, but all appear to be fairly common wherever appropriate sandy and muddy habitats, often intertidal, are found.

Subject editors: Roger J. Safford and Steven M. Goodman

JACANIDAE: ACTOPHILORNIS ALBINUCHA, MADAGASCAR JACANA, TSIKIRANTA, PIRITRY

J. D'Urban Jackson, S. Zefania, and T. Székely

Actophilornis albinucha (Madagascar Jacana) is endemic to Madagascar and distributed in freshwater wetlands in the west and north, mainly in lowland areas. It is found in wetlands with floating vegetation such as water lilies (*Nymphaea stellata* and *N. lotus*, family Nymphaeaceae) and also in lakes with the invasive water hyacinth (*Eichhornia crassipes*, family Pontederiaceae). This bird species occurs in natural and human-modified wetland habitats such as rice paddies, although the relative importance of these habitat types for the long-term persistence of *A. albinucha* is not known.

A recently published molecular phylogeny of extant Jacanidae species using mtDNA fragments indicates that *A. albinucha* is a sister species of *A. africanus* (African Jacana) (D'Urban Jackson et al. 2019). These species are the only two in the genus *Actophilornis*. No subspecies have been recognized for *A. albinucha*.

PLUMAGE AND SEXUAL SIZE DIMORPHISM

Adults of both sexes have a predominantly chestnut-brown back, belly, breast, and wings; white, black, or piebald (see below) hind neck and hind crown; and black underside of neck, with a pale blue frontal shield. Upper tail coverts can be white, rufous brown, or anything in between, and the middle tail feathers are black. The neck plumage is variable among adults: some individuals have almost entirely black necks with only white speckles on the hind neck, whereas others show a clear contrast between the black fore neck and largely white hind neck; some birds with white hind necks show golden plumage at the base of this area. Birds with more white on the hind neck, including golden coloration, tend to also have more white on the upper tail coverts; Figure 13.21 shows such a bird. Studies based on marked individuals through time have not been carried out, but this variation is thought to be age related (Safford 2013q; D'Urban Jackson et al. 2019). The legs and toes are gray to almost blackish,



FIGURE 13.21 *Actophilornis albinucha* (Madagascar Jacana) adult walking on lily pads (*Nymphaea stellata*), Lake Sariaka, Baly Bay protected area. (PHOTO by L.-A. Rene de Roland.)

and toes are elongated, enabling these birds to walk across floating vegetation. Local people report that individuals undergo a simultaneous molt of primary feathers, making them flightless, during which time they swim when disturbed or avoiding predators.

Actophilornis albinucha displays reversed sexual size dimorphism, with females significantly larger than males. The following measurements are based on a sample of 13 females and 22 males unless stated