A decade of monitoring the Critically Endangered Madagascar Pochard *Aythya innotata*: population trends and duckling survival

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Abstract

Factors affecting the breeding success of tropical ducks is an under-researched and poorly understood topic. Here we look at the Critically Endangered Madagascar Pochard *Aythya innotata*, rediscovered in 2006 at a single location, Bemanevika, in northern Madagascar. Local abundance and duckling survival at the site has been monitored since 2010, during which time numbers increased from 20 to 60 individuals. Timing of breeding was variable between years, but in general most broods hatched in the late dry season (September–November). Duckling survival was low (4%, range = 0.1–18% over the years); however, there were three years of unusually high duckling survival (2017–2019), which seem to have been the driver of the population increase. In contrast to most studies of ducklings, we found higher mortality rates as duckling age increased, peaking at 14 days old. We review the available evidence, for and against five main hypotheses, to explain the low breeding success recorded in this population: predation, food availability, disease, weather and timing of breeding. Predation and timing are not strongly supported as causes of low breeding success. Food availability and weather have evidence in their favour but based, on the evidence currently available, are not able to explain the observed population increase conclusively, suggesting no single overarching cause of the problem. Instead, several of the hypotheses may interact. Future monitoring should focus on collection of more data on disease and food availability.

Key words: duckling mortality, endangered species, hatching success, population change.

The Madagascar Pochard *Aythya innotata* was rediscovered in 2006 (Rene de Roland *et al.* 2007); the first sighting of the species for 15 years and the first sighting of more than one individual for more than 40 years (Wilmé 1994). The newly-discovered population was small, and living on a series of small crater lakes close to the village of Bemanevika in northern Madagascar. Initial research showed that breeding success was low but adult survival was high (Bamford *et al.* 2015). No further populations were found, despite extensive searches of nearby wetlands. A captive breeding and translocation programme established a new population 50 km away in 2018.

The Madagascar Pochard belongs to a four-species clade of pochards known as the "white-eyes" (Rene de Roland & Young 2022), assumed to have similar ecology. The only direct study of the species in the wild (Bamford *et al.* 2015) suggests that it feeds almost entirely on macroinvertebrates, particularly larger macroinvertebrates such as Caddisfly *Trichoptera* sp. larvae. Nests are constructed in dense marsh areas, and brooding is done by females. As with many of the diving ducks, the ducklings transition from surface feeding to diving at around two weeks old (Hill & Ellis 1984). There appears to be a peak of mortality at this age (Bamford *et al.* 2015), in contrast to most duck species where duckling mortality rates are high in newly-hatched ducklings but then quickly decline (Baldasarre & Bolen 2006). Bamford *et al.* (2015) concluded that starvation was a likely explanation for the low duckling survival and that the Bemanevika lakes appear to be non-ideal habitat for this species, due to these being deep, cold crater lakes with little emergent and submerged vegetation. The site is a last refuge for the species because, in contrast to the majority of wetlands in Madagascar, it is unaffected by habitat modifications and human activities, such as fishing with nets which may entangle diving birds or reduce their access to feeding areas (Bamford *et al.* 2017).

In addition to food availability, several other hypotheses may explain the observed low duckling survival. In temperate populations, duckling survival is affected mainly by predation and adverse weather (Korschgen *et al.* 1996; Baldasarre & Bolen 2006). The latter could be a problem even in the tropical latitudes of Bemanevika – high altitude (1,600 m a.s.l.) means it is cold in June to August, and there is heavy rainfall in January to March. Predation may be an issue at Bemanevika, with several observations of Madagascar Harrier *Circus macrosceles* catching ducklings at the site. Diseases such as avian influenza and avian cholera may also affect duckling survival (Korschgen *et al.* 1996).

The Bemanevika population of the Madagascar Pochard has been monitored almost continuously since 2010, lacking data only for the years 2014 and 2015. This paper describes trends in numbers and examines hypotheses for observed low duckling survival. In addition to the hypotheses mentioned above (food availability, predation and weather) we also consider general time of year of breeding. Timing can be related to several of the other hypotheses (*e.g.* avoidance of cold/hot times of year, avoidance of predators' breeding seasons, breeding during peak food availability), but there may be reasons why ducks breed at sub-optimal times, such as the flightless moult period dominating adult life-cycles and breeding being a secondary consideration (Cumming *et al.* 2016).

Methods

Study site

Temporary protection established for the Bemanevika Protected Area (14.35°S, 48.58°E) in 2010 by the Government of Madagascar was made permanent in 2015 (Decree No. 2015-782 of 28 April 2015). Of four lakes within the Protected Area, three are classic crater lakes, with deep oligotrophic water (maximum depth = 15 m in Matsaborimaitso; 60 m in Maramaratselegy; 90 m in Andriakanala). These lakes have forest up to the water's edge and no fringing aquatic vegetation along the shoreline. The fourth lake, Matsaborimena, is different, being shallow (maximum depth = 3 m) and turbid, with some fringe marshes. This is where the Madagascar Pochard is most frequently seen and where all breeding attempts up to 2019 were recorded, although during the fieldwork covered in this paper Madagascar Pochard were also recorded breeding on a second lake, at Matsaborimaitso. Bemanevika is 1,600 m above sea level and consequently has a relatively cold climate for the region. July is the coldest month, with a mean maximum temperature of 20°C and a minimum temperature of 9°C, although some nights can drop to 0°C. November is the warmest month, with a mean maximum temperature of 26°C and minimum of 13°C. Average rainfall is 240 cm annually, most of which falls during December–March. Weather data (precipitation, minimum and maximum temperatures) were recorded daily at a research camp located *c.* 2 km from the lakes. The study area is described in further detail in Bamford *et al.* (2015) and Benjara *et al.* (2021).

Fieldwork

Madagascar Pochard monitoring involves four main strands of work: population counts (monthly from 2010 to 2022), brood monitoring (in 2011–2013 and 2016–2022), behavioural observations (2011–2013 and 2016–2022) and food availability surveys (2011–2013 and 2018–2019). Once per month, throughout each year, four observers visited the four lakes simultaneously. Males, females and ducklings were counted, and the total population estimate was determined by summing the counts from each of the four lakes, with the annual maximum count recorded being used as the population estimate for that year. When breeding pairs were active on a lake it was visited more frequently, at least four times per week for 4 h on each occasion, and the ducklings were counted. Because few broods were present at any time, broods were identified from the number and age of the ducklings present in each brood. Fledging was defined as a duckling reaching an age of 60 days. Three times per week at Matsaborimena (and at Matsaborimaitso when breeding pairs were active), Madagascar Pochard behaviour was quantified using scan samples. One scan was conducted every 30 min for a 4 h period (*i.e.* a total of 8 scans), with the sex, group size and behaviour for each bird observed being recorded. Observation periods varied between 06:00–10:00 h, 10:00–14:00 h, and 14:00–18:00 h, so that all daylight hours were sampled. Observations of predation were collected opportunistically during other fieldwork activities.

Adults and ducklings older than 2 weeks mainly feed on benthic invertebrates, although younger ducklings feed on emergent insects. Twenty benthic samples therefore were taken using a Petit Ponar grab sampler (WildCo, Florida, USA), at random positions across Matsaborimena in each month of sampling, to assess food resources for birds at the site. Samples initially were taken monthly from October 2011 to December 2012, then again from October 2018 to July 2019 in response to high duckling survival recorded in 2017 and coinciding with duckling rearing in 2018.

Analyses

Duckling mortality was assessed using the GLM/GAM approach described by Shaffer (2004). This method allows for unequal time gaps between observations, which made it well suited to our data (hereafter we refer to the days between successive observations as the "observation period"). We extended Shaffer's (2004) method to model duckling survival instead of brood survival (Schreiber *et al.* 2016), using binomial regression and scoring each brood as the number of chicks at the start of an observation period and the number surviving until the next observation. A modified logit link function incorporated the length of time between observations. In our data, the shortest gap between observations was 1 day, several were 3 days between observations and there were occasional longer periods when the monitoring team had to be absent from the site. The model allows simultaneous comparison of several variables that may affect duckling survival. In this study, we looked at duckling age, hatching date (estimated from the age of the brood when it was first sighted), total rainfall over the observation period, average minimum temperature and average maximum temperature over the observation period. All variables were fitted as a smoothed function in a Generalised Additive Model, and then as linear functions in a Generalized Linear Model to see which approach provided the best fit. All variables were fitted to a maximum model, with inclusion of variables then assessed using *F*-ratio tests in a backwards stepwise approach, to obtain the most parsimonious model.

Invertebrate abundances were compared using ANOVAs. Predation rates were calculated as the mean number of incidents per hour of observation in which predation or attempted predation of Madagascar Pochard was recorded. An estimate of the total predator threat was then determined by extrapolating this rate to the total daytime hours during the breeding season.

Results

The annual maximum counts of Madagascar Pochard at Bemanevika increased between 2011 and 2021, from *c.* 20 to 60–70 individuals (Fig. 1). Throughout the study, there was a slight but consistent male bias in the adult sex ratio. Breeding was recorded every year on Matsaborimena, and in 2019, 2020 and 2021 on Matsaborimaitso. Breeding activity was recorded in all

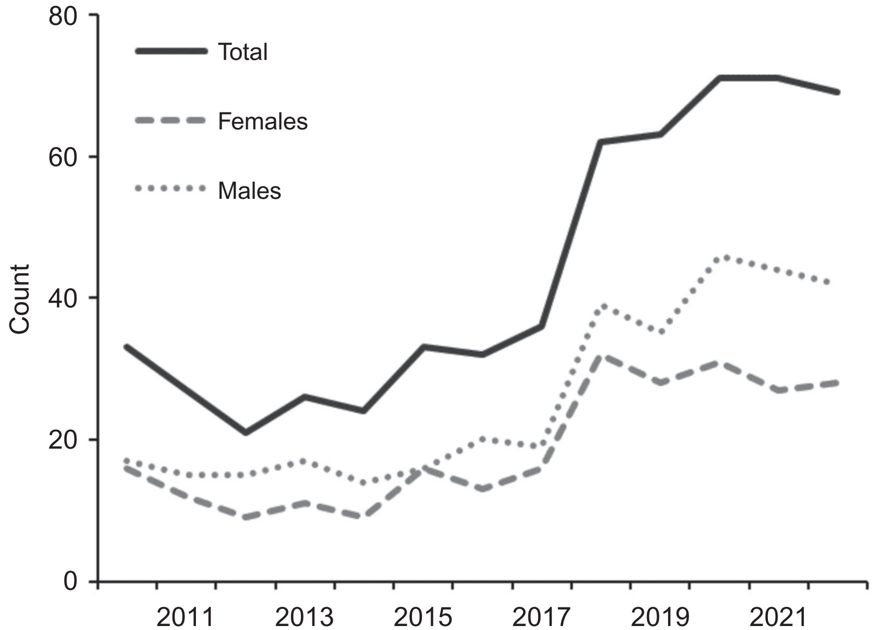

Figure 1. Annual maximum counts of Madagascar Pochard across the four lakes at Bemanevika, Madagascar, from 2010 to 2022.

months across the 10-year period, but not in all months in each year. Over the entire study period, peak hatching occurred in August–October (Fig. 2). Duckling survival was generally low (mean for all years = 4.4% ± 6.2), but varied from a high of 18% in 2017 to a low of 0.1% in 2013 (Fig. 3). Evidence for and against each of the five hypotheses for low duckling survival is given below.

Time of year of breeding and duckling age

Hatching date was associated with duckling survival when fitted to the model without any other explanatory variables included (Fig. 4a). However, there was also an association between duckling survival and age, with daily mortality rates increasing with age up to *c.* 14 days, after which they level off and decline (Fig. 4b). When age and timing of breeding were both included in the model, age was the only significant variable (Table 1).

Weather

There was no association between duckling survival and minimum temperature, but there was a negative relationship with maximum temperature (Table 1), with ducklings suffering higher mortality during hot weather. There was also a negative association between survival and rainfall, with duckling mortality being higher during observation periods with high rainfall (Table 1).

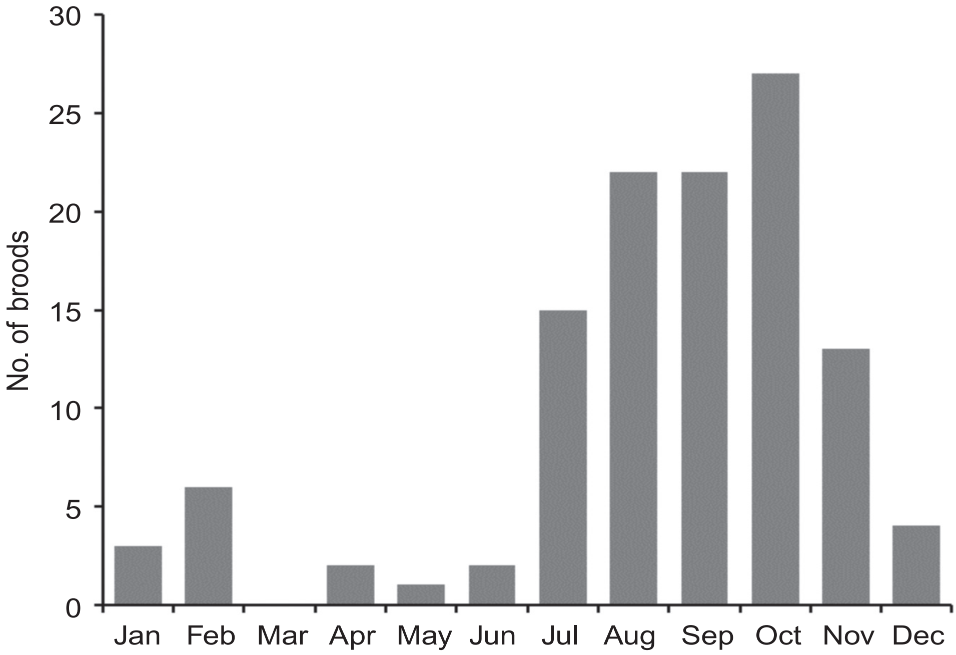

Figure 2. Frequency distribution of hatching dates of Madagascar Pochard broods by month, from 2011 to 2021 inclusive. For each month, the total number of broods first sighted in that month is shown.

Predation

Madagascar Harriers were observed catching Madagascar Pochard ducklings. The number of recorded incidences was small (5 successful catches in 1,200 h of observation), and extrapolation of this rate to the daytime hours throughout all nine breeding seasons when monitoring occurred gave a total of 83 ducklings potentially lost to predation. Whilst this was insufficient mortality for predation to be the main cause of the Madagascar Pochard's low breeding success, it does not rule out a nocturnal predator, and most duckling mortalities seem to occur overnight (Bamford *et al*. 2015). However, six dead ducklings were found on the lake despite low search effort, suggesting a cause of death that leaves carcasses in the lake.

Starvation

Post-mortem examination of duckling carcasses recovered from the lake were consistent with starvation. There was no apparent change in benthic food availability during the years of higher duckling survival. Benthic invertebrate surveys show no change in invertebrate abundance between 2011–2012 (during years with low duckling survival) and 2018–2019 (years with high duckling survival). Chironomidae abundance was 351 ± 52 individuals/m² in 2011/12 and 406 ± 48 individuals/m² in 2018/19 ($F_{1,119}$ = 0.7, P = 0.4). *Trichoptera*

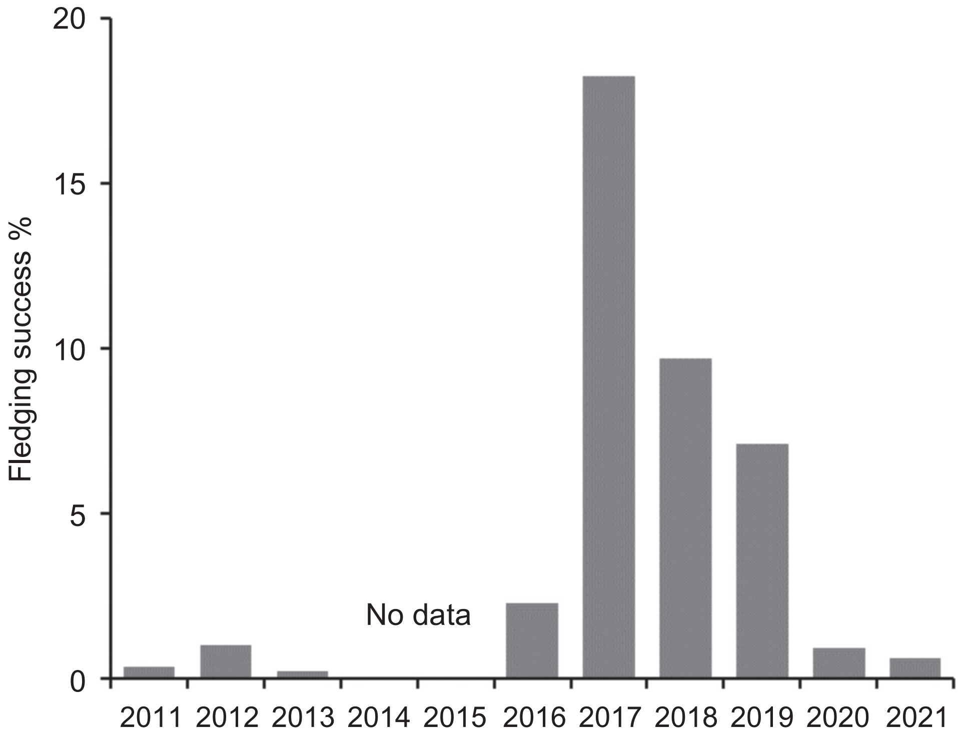

Figure 3. Annual estimates of Madagascar Pochard duckling fledging success from hatching to 60 days old during 2011 to 2021, using the Mayfield method (Mayfield 1975).

abundance also showed no change, at 39 ± 4 individuals/m² in 2011–2012 and 43 ± 4 individuals/m² in 2018–2019 ($F_{1,99}$ = 0.5, P = 0.5). There was variation in the time spent feeding by Madagascar Pochards, with adult birds spending 32% of time diving for food in 2011–2012, 68% of time diving in 2017, 31% in 2018 and 17% in 2019.

Discussion

Although still small, the wild population of Madagascar Pochards has increased substantially since monitoring commenced. It would be tempting to explain this as an effect of the introduction of protected area status to the site since 2010, but the data presented here are not yet sufficient to confirm the connection. The increase appears to be due to a few years of unusually high duckling survival in 2017, 2018 and, to a lesser extent, in 2019. With a return to low duckling survival in 2020, the population has levelled off. If it stays roughly level at around 60–70 individuals, it may be that carrying capacity has been reached. However, if it now declines, the population may be undergoing a cyclical pattern due to local conditions.

Madagascar Pochards at Bemanevika show much variation in timing of breeding

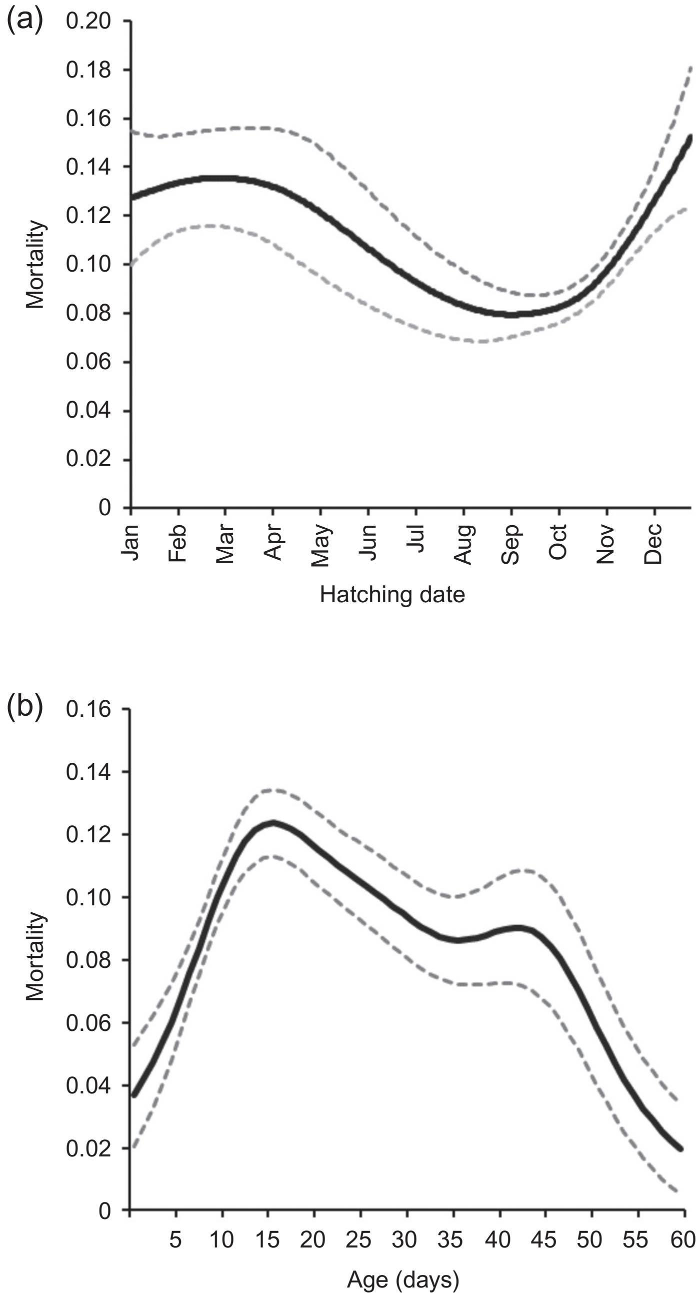

Figure 4. Daily mortality rates of Madagascar Pochard ducklings, estimated using a GAM using data from 2011–2013 and 2016–2022, showing variation with: (a) time of year, and (b) duckling age.

Table 1. Results of the GAM of variables affecting Madagascar Pochard duckling survival between successive observations (the "observation period").

Variable	***F***	**d.f.**	***P***
Duckling age (smooth term)	13.9	5.7	< 0.001
Hatching date (smooth term)	0.8	1	0.3
Rainfall (linear term)	103.9	1	< 0.001
Minimum temperature (linear term)	2.3	1	0.1
Maximum temperature (linear term)	11.9	1	< 0.001

from year to year, which is not unusual for a tropical duck (Cumming *et al.* 2016). Overall, the majority of breeding attempts result in clutches hatching during August–November, at the end of the dry season when temperatures start to increase following the colder winter months (June–August). Breeding during the dry season makes sense for a diving duck, because lakes are at their shallowest at this time of year, and water depth is a major constraint on feeding (Lovvorn & Gillingham 1996). However, the Bemanevika lakes do not vary substantially in depth throughout the year, so this advantage may not apply to this population. Cumming *et al.* (2016) suggest that the timing of the flightless moulting period may be more important to a duck than the timing of breeding, as a failed breeding attempt can be rectified while a failed moulting attempt cannot. The timing of the Madagascar Pochards' moult is more predictable than the onset of breeding, with the moult occurring only in February and March each year (authors' unpubl. data).

Some patterns described by Bamford *et al.* (2015) still appear to hold true. With the exception of the three years noted above, duckling survival rates remained low. In contrast to duckling survival, hatching success in this population has been so high (Bamford *et al.* 2015) that we did not consider it worth monitoring. However, it appears to have declined substantially in 2021 – few broods appeared on the lake despite obvious signs of nesting behaviour by several pairs. Based on two years data, Bamford *et al.* (2015) noted an unusual relationship between duckling age and mortality rate, with daily mortality rates increasing from hatching until 2–3 weeks of age. Now based on nine years of data, this pattern is confirmed. This contrasts with most other studies of wildfowl, mostly conducted in temperate regions, in which mortality rates start high and decline with age (Baldasarre & Bolen 2006). The little data available on duckling survival from tropical regions also shows this pattern (*e.g.* Davis *et al.* 2017; Bonczek & Ringelman 2021). The unusual relationship found in the Madagascar Pochard suggests a different cause of duckling mortality to those found in most (temperate) studies. Younger ducklings would be more susceptible to predation and adverse weather, so the higher survival rate of ducklings under 14 days suggests that these are not the primary causes of mortality in Madagascar Pochards.

None of the hypotheses for low duckling survival were strongly supported. Starvation appears the most likely based on the available evidence, and would explain the observations of carcasses on the lake. However, there is no evidence from the benthic samples for the unusually high fledging success in 2017 and 2018. Benthic food availability did not change between periods of low and high duckling survival, although the data is limited, and there has been no monitoring to date of emergent insect abundance which is likely to be important for younger ducklings. Time spent diving for food was higher in 2017 in comparison with 2011 and 2012, but during 2018 and 2019 diving activity returned to 2011–2012 levels. This leaves the question of why the Madagascar Pochards were able to spend more time diving for food in 2017. The peak in mortality rates coincides with the ducklings transitioning from surface feeding to diving, so both feeding methods may play a role in mortality. One hypothesis is that a lack of emergent insects in the first two weeks of life leaves the ducklings weak. While adult Madagascar Pochards are clearly able to find enough food to survive, it involves more apparent effort than for other *Aythya* species (Bamford *et al.* 2015), due to the depth of the lake and low density of benthic invertebrates. Consequently, only the strongest ducklings may be able to dive to find sufficient food to survive in some years.

Any role of disease is difficult to ascertain at present, as the lack of refrigeration on site makes it difficult to store the dead ducklings that are recovered for further analysis. Storage to date has been in ethanol, but this erases many signs of disease.

There appears to be a possibility that weather affects duckling survival, with rainfall and maximum temperature associated with lower duckling survival over short time periods, but not over entire seasons. Although 2017 and 2018 were not unusually dry years, they were atypically hot. In contrast, 2013 was both cold and dry, yet had very low duckling survival. Predation of ducklings is clearly a problem for the population, in that it definitely occurs, but it seems to be a minor problem and seems an unlikely driver of poor breeding success. The lack of any convincing explanation of the annual variation in duckling survival by these parameters implies that no single factor is solely responsible for duckling survival rates in this population. Instead, several factors may interact to produce the overall situation of generally low duckling survival rates. Food availability, weather and predation may all play a role here. It is difficult to explore these complex interactions even with large datasets (Cumming *et al.* 2016), so it is currently not possible to answer this question with our comparatively small dataset.

The analyses presented here do raise questions about the future of this species. Counts made in 2022 suggest the population was starting to decline, raising the possibility that the increase has no connection to conservation protection but could be related to natural factors. When monitoring started in 2010, numbers also appeared to be in decline, dropping from 30 birds in 2010 to 21 in 2012, and this may be the situation again in a few years' time. Another possibility is that the lakes have now reached carrying capacity, and that numbers will stay level at roughly 60–70 birds. In which case, conservation management of the lake may have been responsible for the increase. Continued monitoring, both of Madagascar Pochard numbers and of variables such as food supply that may be affecting duckling survival rates, will be essential to answer these questions.

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Photograph: Madagascar Pochard, by Andy Bamford.

