

Predicting breeding systems to guide conservation strategies: A kiwi example

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Abstract

The breeding system and mating strategy of a species are at the heart of its behavioral ecology and part of determining its population dynamics. Thus, understanding breeding and mating behavior, and its flexibility, is important for accurate population modeling and successful conservation management. Here, we combine previous work with species-specific data and phylogenetic context to shine the spotlight on the breeding system of North Island (NI) brown kiwi, *Apteryx mantelli*, in a conservation context. The NI brown kiwi is of wide interest as a ratite, which are known for their variable breeding biology both within and between species, and its dire need of conservation management. With the aid of data from a long-term study in a rare, high-density population, we conclude that, although NI brown kiwi have several features characteristic of monogamous bird species (substantial investment in offspring by both parents, long-life expectancy, and well-developed sense of olfaction), it has as many that are consistent with potential for polygamy (uneven quality and distribution of resources, long and asynchronous breeding season, super-precocial chicks, and non-monogamous relatives). Consequently, we suggest that (1) the breeding system of NI brown kiwi is more flexible than has been widely recognized, and (2) further study of NI brown kiwi mating behavior would greatly benefit its conservation planning. Specifically, the prevalence of polygamy will directly affect genetic admixture, maintaining of genetic diversity, and distribution of parentage—all crucial factors influencing translocation success and genetic rescue. We argue that the NI brown kiwi study system could contribute to the increased incorporation of behavioral aspects in conservation management, and we provide suggestions for informative studies that would facilitate this.

KEYWORDS

Aves, breeding strategy, mating system, monogamy, New Zealand, polygamy

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1 | INTRODUCTION

An increasing number of animal populations worldwide require active management to persist. One type of conservation intervention growing in importance is translocations, that is, the movement of individuals to start new, or reinforce existing, populations (IUCN, 2020; IUCN/SSC, 2013). Translocations can result in a boosted population size and growth rate, partly because the introduction of new genetic material can alleviate symptoms of inbreeding depression; a phenomenon known as genetic rescue (Bell et al., 2019; Frankham, 2015; Ingvarsson, 2001; Ralls et al., 2018). Behavioral ecology is directly linked to genetic rescue, and translocation success as breeding unit formation, size, and change overtime are key factors governing if, and how quickly, rescue can be observed (Anthony & Blumstein, 2000; Eberhart-Phillips, 2019; Renan et al., 2018). More broadly, the breeding system and mating strategy both have the potential to impact individual reproductive success, rate of genetic admixture, population growth rate, and ultimately population viability (Adams et al., 2011; Anthony & Blumstein, 2000; Bradley et al., 2014; Hoover et al., 2018; Koenig et al., 2019; Thavornkanlapachai et al., 2019). Consequently, understanding the breeding system of a focal population, and how it relates to factors such as habitat quality and population density, is not only important for understanding the drivers of reproduction-related behaviors but also crucial for conservation management and predicting translocation outcomes. This is particularly true when considering that many species of conservation concern exist in small and isolated populations where they may not be able to display their full range of natural behaviors (see for instance Carrete et al., 2006). In this article, we shine the spotlight on the North Island (NI) brown kiwi, *Apteryx mantelli* (Bartlett), a national icon of Aotearoa New Zealand, that receives extensive conservation attention. By combining theoretical context, previously published empirical studies, phylogenetic background, and species-specific data, we discuss the breeding system of this species, how it links to conservation management, and why there is a large potential for further study in this system.

2 | THEORETICAL FOUNDATION AND EMPIRICAL SUPPORT

Social monogamy was long considered the dominating breeding system in birds (Lack, 1968; Orians, 1969; Wittenberger & Tilson, 1980). However, long-term studies and genetic analyses have shown that (1) polygamy is widespread in birds, and (2) even in species forming social pairs, extra-pair mating and mixed parentage can be common (Brouwer & Griffith, 2019; Griffith et al., 2002; Hughes, 1998; Klug, 2018; Kvarnemo, 2018). In other words, social monogamy is not as common as previously thought, and genetic (or reproductive) monogamy is even less common. Here, we define monogamy as a breeding system where (1) individuals of a population or species form social bonds with one other individual, and (2) typically mate with only this individual, that is, the rate of extra-pair mating is low

or undetectable (cf. Kvarnemo, 2018). This bonding and mating can be maintained long- or shorter-term. The latter, where the rate of divorce and re-pairing is high but usually occurs between breeding seasons, can be referred to as serial monogamy (Culina et al., 2015; Eberhart-Phillips, 2019).

Emlen and Oring (1977) introduced the concept of “potential for polygamy,” suggesting that monogamy is rare and occurs only when a potential for polygamy is non-existent or cannot be utilized. The main component of this potential is the ability of one sex to monopolize either individuals of the opposite sex or enough resources to support breeding with several mates (Emlen & Oring, 1977). Thus, the distribution of resources and mates in space and time is predicted to be key factors determining the potential for polygamy, and which sex will be able to capitalize on it (Emlen & Oring, 1977). In addition, Emlen and Oring (1977) suggested that a long and/or asynchronous breeding season, offspring that do not require biparental care, and phylogenetic predisposition are factors that can increase the potential for polygamy.

Empirical support is stronger for some of the suggested drivers of potential for polygamy than others, but a set of characteristics associated with monogamy in birds is emerging (Brouwer & Griffith, 2019; Griffith et al., 2002; Kvarnemo, 2018). As suggested, habitat limitation and, specifically, low variability in habitat quality seem to be the conditions strongest associated with bird monogamy (Griffith et al., 2002; Kvarnemo, 2018). There is also substantial support that phylogeny and genetic predisposition partly explain the distribution of breeding systems among and within taxa (Björklund, 1990; Mabry et al., 2013; Walters & Garcia, 2016), and the correlation between monogamy and biparental care in birds (Eberhart-Phillips, 2019; Kvarnemo, 2018). For instance, in the genus *Charadrius* (Family: Charadriidae, plovers and dotterels), in which biparental care is facultative, a harsher climate and/or a short (or short remaining) breeding season has been found to increase the prevalence of monogamy, as these factors may lower the chance of successful chick-rearing by a single parent, which increases the gains from biparental care (Eberhart-Phillips, 2019). However, for many other bird species, it remains to be tested whether biparental care is a cause or a consequence of monogamy (Kvarnemo, 2018; Marks et al., 1999).

The role of mate availability for monogamy remains unclear; however, there is support for a link between availability and divorce rate (Culina et al., 2015; Kvarnemo, 2018; Taborsky & Taborsky, 1999). The role of divorce rate, in turn, in defining breeding systems has been debated and is challenging to quantify (Choudhury, 1995). While serial monogamy can involve a high rate of divorce and re-pairing (e.g., Taborsky & Taborsky, 1999), there may be a point beyond which divorce and re-pairing in short succession within the same breeding season is better described as serial polygamy or as a promiscuous breeding system (Culina et al., 2015; Eberhart-Phillips, 2019). Evidence that breeding synchrony affects the prevalence of polygamy is mixed in part because synchrony covaries with migration, environmental variability, and latitude (Brouwer & Griffith, 2019; Kvarnemo, 2018; Spottiswoode & Møller, 2004).

In addition, analyzing the effects of breeding synchrony has been challenging due to the difficulty of accounting for variation within species, wide distribution ranges, and the fact that drivers of genetic monogamy may differ between colony and non-colony breeding bird species (Brouwer & Griffith, 2019). Still, there seems to be a correlation between breeding asynchrony and the rate of polygamy within species (Brouwer & Griffith, 2019).

An important addition to the Emlen and Oring (1977) hypothesis is that the prevalence of monogamy seemingly increases with longevity in birds (Griffith et al., 2002; Kvarnemo, 2018; Leach et al., 2020; Sánchez-Macouzet et al., 2014). A long lifespan suggests the potential for very long-term pair-bonding, and long-term stable monogamy can be expected to render strong selection for the ability to evaluate the fitness and compatibility of potential mates. In support of this, monogamy and a long lifespan have been associated with mechanisms for active and accurate mate-choice, for instance, a well-developed sense of olfaction (Bonadonna & Sanz-Aguilar, 2012; Bonneaud et al., 2006; Caro et al., 2015; Kvarnemo, 2018; Strandh et al., 2012; Zelano & Edwards, 2002).

Taken together, there are a set of characteristics associated with monogamy in birds: (1) low variability in habitat quality, (2) monogamy among closely related species, (3) biparental care, (4) a long lifespan, and (5) mechanisms for active mate-choice; for the remaining discussion in this paper, we refer to this list as the avian monogamy profile. However, we recognize that none of these characteristics, nor any combination of them, prove monogamy or disprove polygamy. Importantly, there is growing recognition that breeding systems are not set in stone but can change overtime and vary within species and populations depending on both biotic and abiotic factors (Ahnesjö & Bussière, 2021; Davies & Lundberg, 1984; Eberhart-Phillips, 2019). To emphasize this flexibility, some authors prefer the term breeding (or mating) pattern over breeding system (e.g., Kvarnemo, 2018; Taborsky & Taborsky, 1999). Importantly, studying groups and species that display several mating strategies and breeding systems in parallel is crucial for furthering our understanding of what drives their evolution, maintenance, and variability (Klug, 2018). One such group of particular interest is Palaeognathae or the ratites (Coddington & Cockburn, 1995; Handford & Mares, 1985; Mitchell et al., 2014).

3 | THE INCREASINGLY LESS ELUSIVE KIWI

The NI brown kiwi is the most common (albeit still threatened) and most researched of the five extant kiwi species (Germano et al., 2018; IUCN, 2020; Robertson et al., 2016). Just like the other species in the genus, NI brown kiwi lay exceptionally large eggs (350 to 500g) and have a long incubation period (about 65–90 days; Colbourne, 2002; Jolly, 1989; McLennan, 1988; Potter, 1989; Sales, 2005). Kiwi have poor eyesight but a very well-developed sense of smell (Corfield et al., 2014) and a huge uropygial gland (Reynolds et al., 2017). These physiological

features suggest that chemical identification and evaluation of, for instance, mates might occur (Castro et al., 2010; Cunningham et al., 2009) and that mate-choice, indeed, seems to be active and disassortative in NI brown kiwi (Undin, Lockhart, Hills, Armstrong, & Castro, 2021c). Kiwi are extraordinarily long-lived, with individuals known to have reached over 40 years and the maximum lifespan suggested to be up to 80 or 100 years (Barlow, 2011; Robertson & Colbourne, 2004; Weiser et al., 2013).

The kiwi genus has been considered elusive due to their nocturnal habits and preference for roosting and nesting in burrows. Leg-fitted radio transmitters have, therefore, been crucial for studying their behavior, ecology, and breeding (e.g., McLennan, 1988; Taborsky & Taborsky, 1991, 1995). During incubation, kiwi leave the nest only once to several times per night, spending only a few hours away from the egg(s). This decline in daily activity during incubation, a further decline during hatching of the egg(s), and a rapid activity increase immediately after eggs are deserted have allowed for the incorporation of an algorithm that can register and interpret activity patterns into the leg-fitted transmitters (wildtech.co.nz/Kiwi.aspx; Colbourne, 2002; Robertson & Colbourne, 2017; Taylor et al., 2014). This algorithm allows conservationists to categorize birds as non-incubating, incubating, deserting, or hatching an egg, using a signal obtained remotely with a handheld receiver. In combination with the super-precocial chicks that receive no food provisioning (Calder, 1979; Colbourne et al., 2005; Taborsky & Taborsky, 1995), these signals allow practitioners to collect eggs from areas deemed unsafe for chicks, raise them in captivity, and later release them back to the wild. This protocol—known as Operation Nest Egg (ONE)—has substantially increased juvenile survival and population recruitment in many kiwi populations (Colbourne et al., 2005; Germano et al., 2018; Kiwis for Kiwi, 2016; Robertson & Colbourne, 2017; Robertson & de Monchy, 2012).

In addition, these activity registering transmitters have greatly increased the potential for studying kiwi ecology, incubation behavior, and breeding success rate (e.g., Bansal, 2020; Cunningham & Castro, 2011; Dixon, 2015; Hiscox, 2014; Wilson, 2014; Ziesemann et al., 2011). This progress is important as many questions remain unanswered, not the least regarding how to optimize kiwi translocations and further incorporate behavior in conservation management (Jahn et al., 2022; Undin, Hills, Lockhart, & Castro, 2021a; Undin, Lockhart, Hills, & Castro, 2021b).

4 | PHYLOGENETIC CONTEXT

Kiwi belong to the ratites together with ostriches (Struthionidae), rheas (Rheidae), emus (*Dromaius* spp.), and tinamous (Tinamidae; Mitchell et al., 2014). Ratites display a wide variety of breeding systems and mating strategies (Coddington & Cockburn, 1995; Handford & Mares, 1985). Ostriches have been observed to breed in monogamous pairs, sequential polyandry, and, commonly, in groups where three female ostriches cooperatively share one male

ostriche and one nest (Kimwele & Graves, 2003). Rheas regularly breed cooperatively with multiple female rheas mating with one or several male rheas and laying eggs in one or several nests, creating a spectrum from polyandry to polygynandry to polygyny (Codenotti & Alvarez, 2001; Handford & Mares, 1985). Emus seem to breed either as monogamous pairs or in a polyandrous system (Coddington & Cockburn, 1995; Handford & Mares, 1985). Tinamous show large variation among species ranging from monogamy to polyandry to cooperative polygyny (Brennan, 2012; Giraldo-Deck et al., 2017; Handford & Mares, 1985; Solano-Ugalde et al., 2018).

Both known extinct ratite groups also had interesting features linked to their breeding behavior: at least one species of moa (Dinornithiformes) had extreme sexual dimorphism with the female being about twice as large as the male, and the eggs of elephant birds (Aepyornithidae) have been found together in large quantities suggestive of shared nesting (Bunce et al., 2003; Olson & Turvey, 2013).

Even within the kiwi genus, a range of breeding systems have been observed (Colbourne, 2002; Eason, 1988; Jahn et al., 2013; Jolly, 1989; McLennan, 1988; Potter, 1989; Sales, 2005; Taborsky & Taborsky, 1991, 1999; Ziesemann, 2011). None of the five extant kiwi species practice female-only incubation; in three species, tokoeka, *A. australis* (Shaw), rowi, *A. rowi* (Tennyson), and great spotted kiwi, *A. haastii* (Potts), incubation is shared between the male and female, and sometimes with additional breeding unit members (Colbourne, 2002; Eason, 1988; Jahn et al., 2013; McLennan & McCann, 1991; Sturmer & Grant, 1988). On Rakiura (Stewart Island; 47°00' S, 167°50' E), the majority of Rakiura tokoeka, *A. a. lawryi* (Rothschild) breed in groups of mixed sexes and ages of up to seven or more individuals (Colbourne, 2002; Taborsky & Taborsky, 1999). Some of these group members have been identified as offspring from previous seasons, and multiple group members partake in incubation (Colbourne, 2002). Based on observations of extra individuals in nests and higher-than-expected parental activity during incubation, some tokoeka on the New Zealand mainland (South Island) may also breed in groups (J. Tansell, unpublished data). In rowi, three types of breeding units seem to occur: monogamous pairs; long-term, stable trios consisting of one adult male and two adult females; and units where juveniles stay around for up to two breeding seasons after hatching (Colbourne, 2002; T. Dearlove, unpublished data). The activity of some staying juveniles has been consistent with partaking in incubation (T. Dearlove, unpublished data). For great spotted kiwi, the number of individuals involved in incubation seems to vary between populations and could possibly be density-dependent (J. Halley & S. Yong, unpublished data). In this species, offspring tend to stay around their parents' nesting area until sexually mature at around four years of age. While the staying juveniles do not seem to partake in incubation (with some possible exceptions; J. Halley, unpublished data), they are frequently found together with their parents and/or newly hatched siblings (Jahn et al., 2013; J. Halley & S. Yong, unpublished data). Taken together, NI brown kiwi have a phylogenetic predisposition for a variety of breeding systems.

5 | SPECIES-SPECIFIC DATA

The onset of the NI brown kiwi breeding season is noticeably asynchronous within years and populations; for instance, on Ponui Island, the laying of the first clutch is spread on average across three months ($n = 9$ –17 pairs per year and 8 years, excluding 2005 and 2006 due to low sample size; Figure 1; Bansal, 2020; Dixon, 2015; Ziesemann et al., 2011). The breeding season then proceeds for about five to eight months, with each breeding pair laying one to three clutches (Bansal, 2020; Colbourne, 2002; Potter, 1989; Sales, 2005; Wilson, 2014). The NI brown kiwi is described as monogamous, even in populations with a male or female bias, but the rate of divorce and re-pairing can vary drastically and seems linked to sex ratio (Colbourne, 2002; McLennan, 1988; Taborsky & Taborsky, 1999). Variation in male strategy and extrapair mating has also been recorded (Taborsky & Taborsky, 1991, 1999; Vieco-Gálvez, 2019; Ziesemann, 2011). Male-only incubation is the norm, but reports exist of isolated incubations by females or a second male (Colbourne, 2002; McLennan, 1988; Ziesemann, 2011). Parental care ends after egg-laying for the female and after hatching for the male (Calder, 1979; Colbourne et al., 2005; Taborsky & Taborsky, 1995).

Despite the large size of the egg, female NI brown kiwi can lay as close as 20 days apart and up to eight eggs per season (Colbourne, 2002; McLennan, 1988). This high productivity is made possible at least partly thanks to (1) female kiwi having two functioning ovaries, which is rare for birds (Kinsky, 1971), and (2) NI brown kiwi being less calcium limited than expected based on egg size thanks to their skeletal composition (Currey & Alexander, 1985; Dennison & Kooyman, 1991), a calcium- and energy-rich diet (Dixon, 2015), and a comparatively thin eggshell (Calder, 1979; Vieco-Gálvez, 2019; Vieco-Gálvez et al., 2020). The ultimate reason for the short time between eggs could be the relatively high hatching failure rate in kiwi (Figure 2; Hiscox, 2014; McLennan, 1988; Potter, 1989; Robertson & de Monchy, 2012; J. Black, unpublished data; R. Toy, unpublished data). If present over evolutionary time, these failure rates have likely generated selection for increased ability to lay replacement clutches (Emlen & Oring, 1977). Frequent laying of replacement clutches has, in turn, been suggested as a key driver for the evolution of male-only incubation (Emlen & Oring, 1977). In light of this, it is particularly interesting that some populations of NI brown kiwi have reported exceptionally high failure rates (Figure 2). Further studies are needed to elucidate if these failure rates are consistent and to exclude the possibility that they are caused by inbreeding depression, which has been found to cause increased hatch failure in other bird species confined to small and isolated populations (Briskie & Mackintosh, 2004). Additional analyses should then focus on whether the lack of female incubation in NI brown kiwi is a cause or consequence of hatching failure; a higher failure rate may have contributed to females reducing their input in incubation to increase their ability to produce replacement clutches (Emlen & Oring, 1977). Alternatively, uniparental care may have evolved first and resulted in the opportunity for females to increase their fitness through additional mating. In either case, the milder climate in its distribution

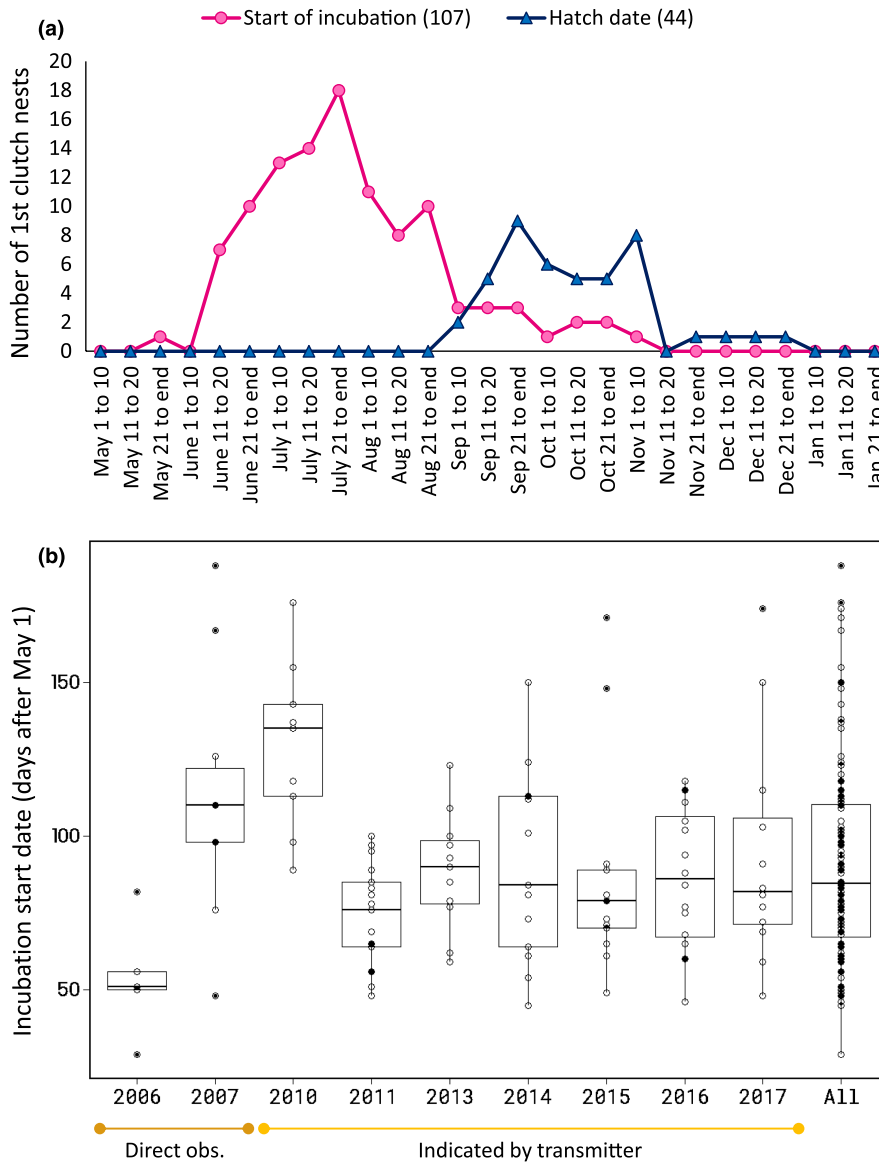


FIGURE 1 Illustration of the timing of the North Island (NI) brown kiwi breeding season on Ponui Island. Timing is defined as the date incubation starts (connected circles in panel a; all of panel b) and the date of hatching (a; connected triangles) of the first clutch. In (a) the number of clutches laid (circles) and the number of clutches hatched (triangles) are summarized across years in 10-day slots. In (b) the variation between and within years in the onset of incubation is illustrated with boxplots highlighting the median date and the quartiles with each data point (nest) represented by one dot. Day 1 refers to May 1. The overall median incubation start date was July 24 but varied between June 21 in 2006 and September 13 in 2010. Years listed indicate the respective breeding season; for instance, an egg hatched in January 2007 falls under the 2006 season. Data combined from Ziesemann (2011), Wilson (2014), Dixon (2015), Bansal (2020), and Castro (unpubl.). Partitions under the graph indicate that two different methods were used to obtain the data: Direct observation of incubating males and leg fitted transmitters indicating incubation

range is likely an important reason why uniparental incubation has evolved in NI brown kiwi, but not in tokoeka, rowi, or great spotted kiwi (Taborsky & Taborsky, 1999).

Territoriality varies notably between NI brown kiwi populations, from low or even absent in areas where birds roam overlapping home ranges, to areas where birds aggressively defend territory borders (McLennan & Potter, 1992; Potter, 1990; Taborsky & Taborsky, 1999; Ziesemann, 2011). This variation could be linked to variable territory quality, which is supported by the fact that foraging success varies with habitat type (Cunningham & Castro, 2011; Dixon, 2015); habitat utilization does not reflect habitat availability (Dixon, 2015; Jamieson et al., 2016); territory size varies with the proportion of preferable habitat (Taborsky & Taborsky, 1995); nests are nonrandomly placed in relation to habitat type (Taborsky & Taborsky, 1995); and hatching success tends to be higher in tree logs compared to other, less spatially restricted, nest types (I. Castro, unpublished data; Wilson, 2014; Ziesemann, 2011). If territoriality is linked to territory quality, it can be expected to be influenced by

habitat and population density, and thus differ between populations (Ippi et al., 2018; Nicola et al., 2015). However, another suggestion is that territoriality in NI brown kiwi is due to mate-guarding by males; this hypothesis is supported by the fact that individual territoriality within populations is linked to pairing status (with unpaired birds having 2–6 times larger home ranges), males show more territorial behavior than females, and territoriality is very low in female-biased populations (Taborsky & Taborsky, 1991, 1992, 1999).

6 | PREDICTED BREEDING SYSTEM

The large investment in the offspring by both NI brown kiwi parents, long lifespan and high pair fidelity in most populations, and highly developed sensory capacity for mate evaluation (in this case olfaction) are all features matching the avian monogamy profile (Table 1; Kvarnemo, 2018). This profile is consistent with previous behavioral studies (Colbourne, 2002; McLennan, 1988; Potter, 1989; Taborsky

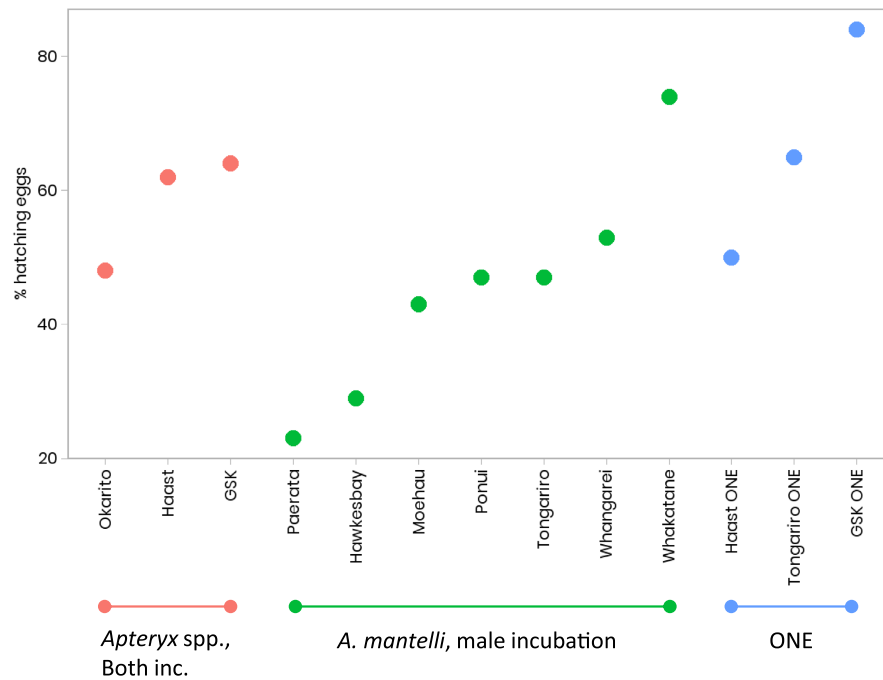


FIGURE 2 Percentage of kiwi eggs successfully hatching in 13 populations. Values are split by incubation strategy and ordered based on success rate. Examples come from three populations of kiwi species where male and female share incubation (rowi from Okarito, tokoeka from Haast, and great spotted kiwi [GSK] from Kahurangi National Park); seven populations of NI brown kiwi (*A. mantelli*) in which the male does all the incubation; three populations in which eggs are collected and artificially incubated in captivity (tokoeka from Haast, NI brown kiwi from Tongariro, GSK from Kahurangi National Park)—A protocol known as operation Nest egg or ONE (Colbourne et al., 2005). Data from McLennan (1988), Potter (1989), Robertson and de Monchy (2012), Wilson (2014); R. Toy, unpublished data; J. Black, unpublished data

& Taborsky, 1999). However, the uneven distribution of high-quality resources, the lack of parental care after hatching, the long and asynchronous breeding season, and the phylogenetic background all suggest that NI brown kiwi have the potential for polygamy (Table 1; Emlen & Oring, 1977).

We suggest that female NI brown kiwi are more to be able to capitalize on such potential because the combination of large eggs, long and male-only incubation, and capacity for rapid relaying likely limits the number of eggs one male can incubate to fewer than one female can lay (Abourachid et al., 2019; Lislevand & Thomas, 2006). In addition, male NI brown kiwi probably have a limited ability for active mate-guarding while they are incubating. Thus, females should have both the reproductive potential and the opportunity to increase their annual fitness by breeding with several males, making the most likely type of polygamy for NI brown kiwi polyandry. Specifically, we suggest that the male-only incubation period is long enough to enable the female to generate and maintain social bonds and mate with more than one male. While the eggs will be multiple weeks apart in age, the nests of both (or all) males will overlap in time. As the females do not regularly partake in incubation, we suggest that the females spend a similar investment in both (or all) nests. If this is the case, we suggest that this system is best described as social polyandry. This is compared to extra-pair mating, which suggests an unequal investment in the eggs and the relationships with the males (Brouwer & Griffith, 2019), or to serial polygamy, in which females would have

multiple, non-overlapping, partners within the same breeding season (e.g., Eberhart-Phillips, 2019).

This suggestion presumes the availability of non-incubating males, and such “floating” males have been observed in multiple populations (Dixon, 2015; Taborsky & Taborsky, 1999). At the same time, a previous study found no evidence for polygamy in a male-biased or a female-biased population (Taborsky & Taborsky, 1999), suggesting that mate availability alone is not enough to generate polygamy potential for this species. At the same time, a recent study found high levels of mixed parentage among eggs incubated by the same NI brown kiwi males in a highly managed population (Vieco-Gálvez, 2019), and other studies have found examples of extra-pair mating (Taborsky & Taborsky, 1999; Ziesemann, 2011), suggesting that the occurrence and frequency of polygamy likely differ between populations.

7 | CONSERVATION IMPLICATIONS

There is growing recognition of the need for multifaceted approaches to conservation. As part of this, the better our understanding of breeding systems and what drives inter- and intraspecific variation grows, the better our ability to develop accurate conservation management plans becomes. We argue that the behavioral aspect of conservation has rarely received the needed attention, and the NI brown kiwi is an example of this; despite a more flexible breeding

TABLE 1 List of breeding and life-history features consistent with potential for polygamy or the typical profile of a monogamous bird species, and how they relate to North Island brown kiwi biology (based on Emlen & Oring, 1977; Kvarnemo, 2018)

Polygamy potential	Support in North Island brown kiwi
Uneven distribution of resources	Yes - both distribution and quality uneven
Uneven distribution of mates	No - grouping of males or females does not occur ^a
Long/Asynchronous breeding season	Yes
No need for biparental care	Yes - female care ends at laying and male at hatching ^b
One sex is limiting	Yes - number of eggs male can incubate < number of eggs female can lay
Monogamy profile	Support in North Island brown kiwi
Low habitat variability	No - both distribution and quality uneven
Need for parental care	Yes - big investment in offspring by both male and female
Longevity	Yes - over 40 years
Mate-choice mechanisms for instance through olfaction	Yes - a well-developed sense of smell

^aBut females will spend more time active during the incubation season.

^bChicks frequently stay around the nest and/or dad for days to weeks after hatching. No active parental care, such as food provisioning, occurs during this time; still, it is possible that chicks experience benefits by staying such as reduced predation or lowered energy expenditure.

system being suggested for decades (Taborsky & Taborsky, 1991, 1999; Ziesemann, 2011), the national and regional conservation management and translocation guidelines treat NI brown kiwi as a monogamous and highly faithful species (Craig et al., 2011; Germano et al., 2018; Jahn et al., 2022; Scrimgeour & Pickett, 2011).

Translocations are of growing importance for conservation management for many species, including NI brown kiwi. Thus, recognizing the potential effects of a species breeding system is important for several reasons. (1) Partner swaps, mixed parentage, and polygamy can increase the rate of admixture, alleviation of inbreeding depression, as well as introgression of beneficial gene variants following supplementary translocations (also referred to as reinforcement translocations; Rick et al., 2019; Vila et al., 2003; Weiser et al., 2013). In other words, it can increase the chance of genetic rescue (Bell et al., 2019; Frankham, 2015; Ingvarsson, 2001; Ralls et al., 2018). (2) When polygamy results in some or most individuals mating successfully with more than one partner, genetic diversity is retained thanks to a higher rate of gene flow compared with monogamy. This flow reduces the likelihood of population structuring, and thus increases the number of potential source populations for translocations even if it is deemed desirable to strive for minimal genetic difference between the translocation source and target (Eberhart-Phillips, 2019; Jackson et al., 2017; Küpper et al., 2012). In addition, this retention of genetic diversity means that polygamy will determine the rate at which additional restocking translocations are needed (Weiser et al., 2013). On the other hand, in other types of polygamy that restrict successful breeding to a small number of individuals, such as leks or harems, the effective population size and thus the genetic diversity will be reduced compared with monogamy (Nunney, 1996; Stiver et al., 2008). (3) Directly linked to the latter, the prevalence of polygamy may compensate for a small founder population size. Among other things, this compensation means that the current strict cut off at a founder size of 40 individuals to consider a historic translocation successful (Germano et al., 2018; Jahn et al., 2022) may need to be re-evaluated (Undin, Hills, Lockhart, & Castro, 2021a; Undin, Lockhart, Hills, Armstrong, & Castro, 2021c;

Undin, Lockhart, Hills, & Castro, 2021b). (4) The higher the prevalence of polygamy, the harder it will be to assume relatedness between individuals based solely on the identity of the incubating male (cf. Vieco-Gálvez, 2019). (5) The presence of polygamy will further complicate the long-sought-after relationship between the standardized call count surveys and the number of breeding units, population growth rate, or carrying capacity. Thanks to these potential implications of polygamy in NI brown kiwi, we suggest that, until there is sufficient knowledge to account for variation in breeding behavior, genetic testing should be utilized more than is currently the case, both before and after translocations.

Furthermore, a major cause of population decline in NI brown kiwi, as well as many other species, is predation by introduced mammals (Glaser & Allerby, 2010; Heinsohn et al., 2019; McLennan et al., 1996; Wilson et al., 1998). When such predation risk is related to size or time spent incubating, mortality can be unevenly spread between the males and females, resulting in a biased sex ratio (Glaser & Allerby, 2010; Heinsohn et al., 2019; Wilson et al., 1998). In some bird groups, the sex ratio has been linked to the breeding system (e.g., Safari & Goymann, 2021), and in the swift parrot, *Lathamus discolor* (White), the uneven sex ratio caused by predation has been found to increase extra-pair mating (Heinsohn et al., 2019). In turn, this form of polygamy has been found to reduce the number of successful fledglings per swift parrot nest, making an already dire situation worse for this critically endangered species (Heinsohn et al., 2019). This case highlights that the effects of introduced predators can go beyond the direct reduction of population size and distribution and once again emphasizes that predator control should remain a cornerstone in NI brown kiwi conservation, with translocations being an important complement.

8 | FUTURE STUDIES

We suggest that there is great potential in NI brown kiwi as a study system to provide vital information on breeding behavior and how

to incorporate it into conservation management for three reasons: (1) the range of population sizes and densities are still available in NI brown kiwi with populations ranging from over 100 to less than one bird per 100ha; (2) translocations of NI brown kiwi have occurred for over 100 years and, for many populations, the founder size, composition, and timing is known; (3) methods and infrastructure for pre- and post-monitoring are already established. We suggest that an initial focus is needed on how breeding systems and mating strategies change with habitat alterations and population density. This work was initiated by Taborsky and Taborsky (1999) who compared three NI brown kiwi populations with different densities and sex ratios. An important next step would be to increase the sample size (both within and among populations), the range of densities evaluated (in particular to populations with even higher densities), and the geographic spread within the North Island. In this way, the effects of climate, partner availability, density, and habitat on extra-pair mating, territoriality, as well as breeding unit composition and stability could be further investigated.

Mate-choice is closely linked to the breeding system, directly impacts translocation outcomes (Undin, Lockhart, Hills, Armstrong, & Castro, 2021c), and has likely been affected by anthropogenic impact even more than breeding systems. Thus, studies of mate-choice in relation to lowered population density, habitat modification, and reduced connectivity, are also important for improving conservation management. We suggest that the lack of distinguishing morphological features, the long lifespan, and the highly developed olfaction, in combination with the three reasons listed above, make NI brown kiwi an interesting study system for mate-choice as well. Lastly, we suggest that there could be substantial benefits of utilizing genomics (i.e., genome wide genetics) in the studies of NI brown kiwi breeding (Galla et al., 2020; Kardos et al., 2016; Oylar-McCance et al., 2016; Putman & Carbone, 2014; Semenov et al., 2017; Thavornkanlapachai et al., 2019; Undin, Lockhart, Hills, Armstrong, & Castro, 2021c). For instance, individual and population-level genomic make-up can be used to analyze effective population size, admixture, breeding behavior, and mate-choice over time, as well as the effectiveness of conservation interventions (Galla et al., 2020; Semenov et al., 2017; Thavornkanlapachai et al., 2019; Undin, Lockhart, Hills, Armstrong, & Castro, 2021c). Another example is that genomic traces of fluctuations in population size and diversity can be related to breeding system and reproductive output to increase our understanding of inbreeding depression (Kardos et al., 2016).

9 | CONCLUDING REMARKS

The potentially extensive impact of breeding systems and their variability highlights the need to incorporate breeding biology into the already challenging field of predicting translocation outcomes (Undin, Hills, Lockhart, & Castro, 2021a; Undin, Lockhart, Hills, & Castro, 2021b). As described above, resource distribution is one of the main factors determining breeding systems, and breeding

systems as well as mating strategies can change with population density, habitat, and/or availability of territories and mates (Carrete et al., 2006; Griffith et al., 2010; Heinsohn et al., 2019; Pribil & Searcy, 2001; Walker et al., 2008). Thus, concern is warranted for an ongoing, worldwide shift in breeding behavior caused by anthropogenic habitat alteration, destruction, and fragmentation (Banks et al., 2007; Buchholz et al., 2019; Candolin & Wong, 2016; Caro & Sherman, 2011; Lane et al., 2011; Winiarski et al., 2017). Consequently, increasing our understanding of the drivers for and the conditions under which different breeding systems and mating strategies evolve, take effect, and change is urgently needed to assist conservation management, save threatened species, and maintain biodiversity—including behavioral diversity (Griesser et al., 2017; Klug, 2018; Koenig, 2017; Koenig & Dickinson, 2016). We hope that we have spiked interest and recognition for the importance of further investigations of NI brown kiwi breeding biology, both because the flexibility in the breeding system of NI brown kiwi may work in the favor of conservation management and because there is great potential in utilizing this study system.

AUTHOR CONTRIBUTIONS

MU undertook the analysis, prepared the original draft, and led the visualization of the data. IC led and supervised the investigation, the fieldwork, and the acquisition of funding, as well as developed the experimental design and undertook the administration of the project. MU and IC jointly conceptualized, reviewed, and edited the manuscript.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data for this article is available in the cited literature and/or directly in the article figures.

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