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The mating system and stability of pairs in kiwi *Apteryx* spp.

Barbara Taborsky and Michael Taborsky

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Different populations of kiwi *Apteryx* spp. live in very different habitats and climatic conditions, and they vary greatly with regard to population densities and sex ratios. Populations also differ remarkably in their social and mating patterns. By comparing four populations, we asked whether kiwi mating systems are primarily shaped by the availability of mates as caused by different operational sex ratios (“environmental polygamy potential”), or whether they depend on the costs and benefits of desertion by either sex from parental care, especially on the limitations to desertion due to high precopulatory investment (“parental limitation”).

Most kiwi have long-term partnerships and very high partner fidelity, but in one population half of all pairs split each year. This is a relatively dense population with a strongly female-biased sex ratio and a complete lack of territorial behaviour. We argue that pair stability and territoriality are related in kiwi, and that the loss of territoriality and the high divorce rate in this divergent population result from the female-biased sex ratio. Data analyses did not reveal any reproductive advantage from divorce and re-mating with a different partner in kiwi. We suggest that divorce results from the interaction of surplus females with paired males and is hence “forced” upon the pair.

Our analyses of social systems of the four populations of kiwi suggest that both territory defence and the degree of polygamy depend primarily on parental demands and not on the distribution of resources and mates. Hence, we regard the “parental limitation hypothesis” as being the more adequate one to explain mating patterns in kiwi.

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The endemic New Zealand kiwi may be used as a paradigm for extreme parental investment, with females producing huge and energy-rich eggs that are incubated solely by males for about three months (McLennan 1990). They were thought to live solitarily on territories and to have life-long monogamous pair bonds (Colbourne and Kleinpaste 1983, Taborsky and Taborsky 1991). However, recent field studies revealed a remarkable variation in mating and social systems as well as deviations from a solely paternal incubation (Potter 1989, Sturmer and Grant 1988, McLennan and McCann 1991a, Taborsky and Brugger 1994).

Due to their extreme parental investment, kiwi offer a unique opportunity to investigate the role of pre- and postcopulatory investment as determinants of their mating system. There are mainly two, non-exclusive lines of argument to explain the evolution of mating

systems (Davies 1991). (a) Mating systems may depend primarily on the distribution of the limited sex, which may depend in turn on the distribution of limiting resources. In this case, the environment determines the polygamy potential in a population (Emlen and Oring 1977). (b) In species which provide care, mating systems may depend particularly on the costs and benefits of desertion by either sex (Trivers 1972, Maynard Smith 1977, Sargent and Gross 1986, Davies 1991). The necessity that offspring are reared by one or both parents, the alternatives mates have in case of desertion, and the timing of parental input (i.e. pre- or postcopulatory) affect fitness payoffs of parents and hence the evolution of sexual strategies. Additionally, the degree by which precopulatory investment of one sex (i.e. the production of gametes) limits its broodcare abilities may influence the likelihood that parental care is shown by this or the other sex.

If mate distribution is primarily shaping reproductive strategies of kiwi we would expect the mating system to vary with the respective operational sex ratio of a population ("environmental polygamy potential hypothesis"). In populations with female-biased operational sex ratios polygyny should occur, whereas in male-biased populations polyandry should be favoured. Balanced sex ratios should favour monogamy.

Alternatively, under the "parental limitation hypothesis" we would expect that the mating system depends mainly on the relative limitations of the two sexes due to parental investment. For example, in bird species with sole paternal care often polyandry is found (Davies 1991), as females are free to lay more eggs for other males while their first partner is incubating. If females invest heavily in each clutch, however, they may simply desert from parental care because of energetic limitations, in order to recover while their partner incubates. In this case, monogamy should be expected.

Among species maintaining long-term partnerships, the rate of divorce (*sensu* Choudhury 1995) is an important component of the mating system, with a strong impact on the fitness of one or both partners (e.g. Black 1996). In non-migrating birds, there are primarily two reasons why divorce may occur (Choudhury 1995): (a) Improved reproductive success; divorce is initiated by one or both partners and results in increased fitness in at least one partner, either because of better compatibility with a new partner (e.g. Coulson 1972, Coulson and Thomas 1983, Rowley 1983), or because of the better quality of a new partner and/or territory (e.g. Diamond 1987, Harris et al. 1987, Ens et al. 1993). There may be a third possibility to improve reproductive success; divorce may be initiated because a new partner is in an advanced reproductive state compared to the old part-

ner that has just invested in a clutch, therefore, the new partner may be ready to reproduce at an earlier time. (b) Salvage strategies; divorce is forced upon the partners either by the action of competing conspecifics, a mechanism we termed "forced divorce" (see Choudhury 1995), or by accidental separation (Owen et al. 1988, Forslund and Larsson 1992). The occurrence of salvage strategies (i.e. non-adaptive divorce) is suggested in cases in which no advantage for either of the divorced partners can be detected.

In this paper, we compare four populations of kiwi living under different ecological conditions, to analyse what may primarily determine their mating and social systems. We put special emphasis on the sex ratio, and on the significance of pair stability and divorce. The four studied populations belong to the species *Apteryx mantelli* and *Apteryx australis*, which are morphologically extremely similar and were regarded as being one species (*Apteryx australis*) until recently (Baker et al. 1995).

Methods

Table 1 gives basic information on the populations investigated in four independent studies, which provided the data for our analyses. If not otherwise cited, data are taken from the references listed in Table 1. Altogether, the data were collected from 51 males and 37 females during a total period of 12 study years. Three of the four populations belong to *A. mantelli* and live on New Zealand's North Island. The fourth population belongs to *A. australis* and lives on Stewart Island. As these two species resemble each other very closely morphologically and ecologically, they have only been recognized as two species on genetic evidence (Baker et

Table 1. Basic information about the four kiwi populations compared in this study.

Study site	Waitangi	Paerata	Hawke's Bay	Stewart Island
Abbrev. used in text	WAI	PAE	HAW	STE
Region (New Zealand)	North Is.	North Is.	North Is.	Stewart Is.
Location	35°15'S 174°02'E	35°47'S 174°02'E	39°06'S 176°44'E	47°09'S 167°45'E
Study years	1985-87, 91	1985-87	1984-85	1988-90
Climate	warm temperate	warm temperate	warm temperate	cold
Habitat	pine forest	secondary bush	primary forest	tussock grassland
Kiwi/100 ha	17.1	19.3	1.0	40.8
Ratio males: females	1:0.6	1:1.6	1:1.7	1:1.2
Data included from				
males:	31	7	3	10
females:	14	13	5	5
Sources	Taborisky and Taborisky (1991, 1992); own unpubl. data	Potter (1989)	McLennan et al. (1987), McLennan (1988)	Colbourne unpubl. reports 1988, 1989, 1990; this study

Table 2. Range sizes of paired kiwi (ha) as estimated by an adaptive kernel method and by the minimum convex polygon method (MCP); the last two columns give average maximum percentages by which each target bird overlapped the range of any of its neighbours. Successive lines within each data set are: (1) medians; (2) interquartile ranges; (3) sample sizes.

	Sex	Range size		Max.% overlap with		
		Kernel	MCP	partner or group mb	neighbours of same sex	neighbours of other sex
WAI	males	6.6	8.1	85.2	21.1	3.7
		4.2–7.7	5.6–9.4	69.2–89.5	9.1–51.8	0.2–10.1
	females	14	15	8	8	8
		7.8	10.9	62.3	11.2	30.4
		5.9–11.0	8.8–12.1	10.8–23.7	12.0–46.9	14.3–45.6
		12	9	7	8	8
PAE	males	–	35.3	60.5	52.6	61.6
		–	32.7–63.5	53.8–70.2	50.9–60.7	50.4–77.8
		–	10	10	10	10
	females	–	27.8	62.5	58.0	59.3
		–	19.9–60.8	50.3–68.4	41.7–66.7	42.3–72.8
		–	13	13	13	13
HAW	males	–	25.4	92.3	9.1	3.3
		–	21.6,38.8	84.8,92.3	5.6,17.6	1.8,5.8
		–	3	3	3	3
	females	–	41.0	65.2	6.1	6.5
		–	32.5,41.1	57.2,80.1	1.5,6.7	2.5,8.2
		–	3	3	3	3
STE	males	5.6	5.7			
		4.2–7.3	3.7–7.6			
		4	6			
	females	5.3	5.4			
		3.7–7.7	4.7–7.9			
	group member	4	5	55.0	3.8	8.1
			51.4–74.2	6.4–11.1	1.6–16.5	
			5	4	5	

al. 1995). Birds of the Stewart Island population were about 13% larger and 26% heavier than those on the North Island. The densities and sex ratios given in Table 1 do not necessarily reflect the situation of undisturbed, natural populations as during the last century kiwi have been exposed to a substantial predation pressure by introduced mammals (e.g. King 1984, Taborsky 1988).

Telemetry was used in all four studies to obtain data about space use and social organization (for methods see McLennan et al. 1987, Potter 1989, Taborsky and Taborsky 1991, 1992). Unless stated otherwise, we present only data which are comparable between the studies with regard to methodology. Range sizes given have been estimated by using an adaptive kernel method (see Taborsky and Taborsky 1992) where possible, and additionally by the minimum convex polygon method (MCP; Mohr 1947) for comparative reasons. The former method gives a much more reliable estimate of kiwi ranges (Taborsky and Taborsky 1992; see the methodological review of Worton 1987), but only MCP estimates were available for all four populations. Sex ratios and densities were calculated from numbers of transmitter-banded kiwi inhabiting the respective study areas. Birds occupying ranges which were only partially included within the defined study areas were counted proportionally. Values given for PAE (see Table 1 for

abbreviations) deviate from the ones given by Potter (1989) but were recalculated by use of this proportional representation (M. Potter pers. comm.), to allow a direct comparison between populations.

Kiwi are nocturnal, cryptic and shy birds that usually cannot be studied by direct, visual observation, especially if they dwell in dense undergrowth. Therefore, a range of methods and criteria had to be employed to determine pair bonds. In the WAI study, behavioural information was obtained by recording all calls and sounds made by individual birds during nocturnal observation periods (Taborsky and Taborsky 1992). This was supplemented by occasional visual observations with the help of night vision equipment. Kiwi were considered to be paired if their ranges overlapped largely (see Table 2) and they were observed to interact socially by pair calling, a certain grunting display and/or if roosting together (Taborsky and Taborsky 1991). Similar criteria for determining pair bonds were applied by J. A. McLennan (pers. comm.) in HAW and by Potter (1989) in PAE. Members of a former pair were regarded to be divorced only if both were still separated from each other after 2 to 3 months, or when at least one member had re-mated, and its former partner was still alive.

In WAI, infrared light sensors were installed at nest entrances and combined with data loggers to determine

the incubation times of males. On STE, the presence of transmitter-tagged males and females at nests was determined several times per day by using telemetry. Gravid females of the Waitangi and the Stewart Island populations were monitored closely with the help of telemetry before egg-laying to find out in which nests eggs were laid.

Size measurements and weights were taken when the birds were captured. Weight comparisons between individuals, sexes and populations always refer to non-reproductive weights. In the WAI and STE studies, nine morphometric measures were taken: three different measures of tarso-metatarsus length, minimum and maximum width of tarso-metatarsus, length of middle toe, length of skull, length of beak, width of beak at its basis. From these measures, a suitable estimate of structural body size for inter-population comparisons was chosen using three criteria: (i) low measurement errors, (ii) a strong relationship to lean body mass (as measured by the Oxygen Dilution Method with the help of the injection of water labelled with a known amount of O^{18}), which is itself a reliable estimate of structural body size, and (iii) the existence of comparable measurements from the different studies. Minimum tarsus width turned out to fit these three criteria best and was hence chosen as a measure of body size. We calculated a condition index

$$\frac{\text{weight}^x}{\text{min. tarsus width}}$$

with the exponent "x" removing the allometric influence of size variation on the condition factor; "x" is the reciprocal of the slope found by relating the logarithm of body mass to the logarithm of minimum tarsus width.

We used medians and interquartile ranges as descriptive statistics and calculated non-parametric tests if data differed significantly from normal distributions or the sample sizes were too small to test for deviations from normal distributions. Otherwise, means, standard deviations and parametric tests were used. We used two-tailed tests unless otherwise mentioned.

Results

Sex ratio

In WAI, there were nearly twice as many males as females, whereas the populations in PAE, HAW and STE were female-biased to various degrees (Table 1).

Mating system

There was no evidence for polygamy from the spacing and calling patterns in WAI, PAE and HAW ($N = 16$, 16, and 6 "pair years"), irrespective of the male- or female-biased sex ratios of these populations. Close monitoring of females in WAI showed that they laid eggs in nests of only one male partner ($N = 20$ eggs of 10 different females, 15 nests). There were unpaired, territorial males adjacent to at least five of these females during the production of 11 eggs. Also, successive clutches were only produced for the same male partner to replace abandoned clutches ($N = 4$ cases).

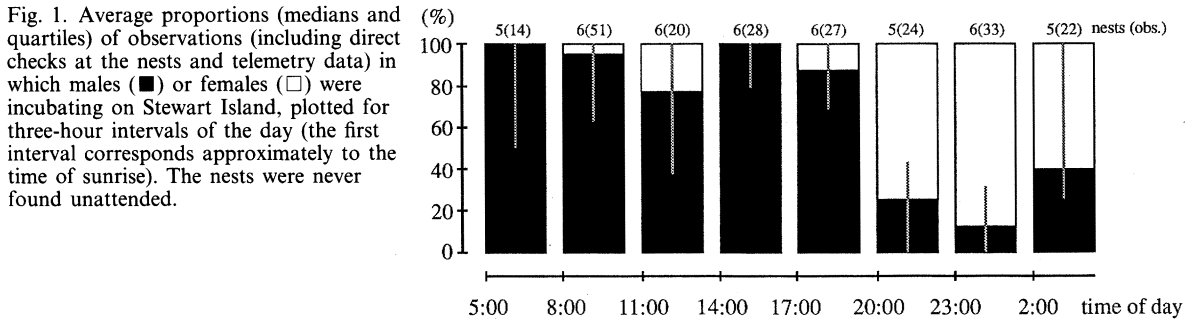
On STE, groups of adult and juvenile birds shared common ranges. Although this population had the least biased sex ratio, polygyny may have occurred. Three out of nine groups contained two adult females and one adult male during the 1990 breeding season. One of these trios roosted together in the same shelter site once in 1990. R. Colbourne (pers. comm.) found a freshly hatched chick and a young of about 4 months of age together with a pair; it is very unlikely that one female had produced both young because in this case she would have laid an egg only about a month after she completed incubation of her previous egg (on Stewart Island, females share in incubation; see below).

Territoriality

Ranges of neighbouring kiwi pairs were nearly exclusive in WAI, HAW and STE (Table 2) and were regarded as territories. Birds of these populations defended their territories by long distance calls and only rarely by direct interactions (McLennan et al. 1987, Taborsky and Taborsky 1992, this study). Territories of partners overlapped much more than with paired neighbours of the opposite sex (Table 2; Wilcoxon matched-pairs signed-ranks tests: $P \leq 0.01$, $N = 8$ males; $P \leq 0.05$, $N = 7$ females). In PAE, ranges of partners overlapped as much as ranges of neighbours did (Table 2; Wilcoxon tests: $P > 0.1$, $N = 10$ males; $P > 0.1$, $N = 13$ females), and they shifted with time (see cumulative range size plots of Potter 1989). Hence, these ranges were not regarded as territories.

Parental investment

In the three North Island populations, females were never found incubating and, with few exceptions, did not brood chicks. During the incubation periods, WAI males left their nests for nocturnal feeding trips that lasted between 5.3 h ($= \bar{x}$; $SD = 1.2$, $N = 4$ males, 20 nights in total) during the first third of incubation and 2.9 h ($SD = 0.3$, $N = 4$ males, 32 observed nights) during the last third. On average, eggs were left unattended



for 3.8 h (\bar{x} ; SD = 1.2, N = 9 males; 89 observed nights), 3.6 h (SD = 1.3, N = 13 males) and 4.9 h per night (SD = 1.6, N = 16 observations of a maximum of 3 males) in WAI, PAE and HAW, respectively (means of the means of individual males are given for WAI and PAE, and the mean of pooled data for HAW), which compared to an average active period of 11.5 h (onset of activity: N = 9 birds, each observed twice on average; end of activity: two birds, each observed once), 8.5 h (SD = 1.1, N = 9 birds) and 7.4 h (SD = 1.6, N = 7 observations) for non-incubating kiwi of the three populations, respectively, during comparable periods of the year. STE kiwi were incubating in all 62 cases when the six nests were directly checked. These checks were spread over different times of day and night, suggesting continuous incubation. In this population females shared in incubation, and similar to males they had large broodpatches. Males incubated during daytime and for parts of the night, which added up to about two thirds of total time; females took over the remaining third, mainly during the night (Fig. 1).

The difference in female share of broodcare between North Island and Stewart Island Kiwi coincides with a difference in clutch sizes. Nest checks revealed that on the North Island, clutches consisted primarily of two eggs (WAI: 95%, N = 19; PAE: 50%, N = 12; HAW: 100%, N = 6), the rest were one-egg clutches. On STE, only one-egg clutches were found (N = 3 successful and 2 failed clutches) in the 1990 breeding season.

Stability of pairs

In WAI and HAW, all adult pairs were stable across years (Table 3) and also stayed in the same territories (WAI: N = 6 males and 6 females; HAW: N = 3 males and 3 females, each bird observed in at least two years).

We used the equation

$$D = \sum_{i=0}^{20} s^i$$

to calculate the average duration D of a pair bond under the assumption of a constant rate of divorce,

Table 3. Pair stability and divorce in the four populations studied (for references see Table 1; for WAI, data are also included from Colbourne and Kleinpaste 1983). Filled circles (●) refer to the observation of a pair with individually recognized members in a given year or reproductive season. Rows represent histories of different pairs, columns represent successive years or reproductive seasons. Two successive filled circles in a row show that the same pair members are still paired. D = divorce, †one partner died; the columns following these events shows which partners were observed to have re-mated. * = either trio or mate change.

Year	1	2	3	4	5	6	7
WAI	●					●	●
	●	●				●	
	●		● †			♀	
	●		● †			♀	
	●	●					
	●	●					
PAE	●	●	●				
	●	●					
	●	●					
	●	●					
	●	● D	♂				
	● D	♂+♀					
	● D	♂+♀					
	● D	♀					
	● D	♀					
	● D	♀					
	● †	♂					
HAW	●	●					
	●	●					
	●	●					
STE	●	●	●				
	●	●					
	●		● Trio?				
	● Trio		● Trio				
	●	●					
	●		●				
	●		*				

where s is the proportion of pairs remaining stable from one year to the next and i [0, 20] represents the reproductive lifespan of a kiwi, which we assumed to be 20 years. Even when allowing for 5% of undetected divorces, the average duration of a pair bond would still exceed 13 years in WAI and HAW. No clear case of mate switching was observed also on STE (Table 3) and all observed adults remained on their territories (7 males and 8 females, observed in at least two years; R. Colbourne pers. comm. and own obs.). In PAE, the divorce rate from one year to the next was 50% (Table 3), the average duration of pair bonds (D) as calculated with equation (1) was two years ($s = 0.5$). Re-mating occurred in WAI and PAE after the death of a partner (3 cases), and in PAE following divorce (6 cases, Table 3).

If divorce serves to obtain a better partner, one would expect that the new partners would have higher condition factors than their predecessors, as large body mass relative to size appears to indicate partner quality in kiwi: (i) in WAI, only heavy males or males with a high mass/size ratio were paired (comparison paired vs. unpaired males: tarsus width: $P > 0.1$, $N = 16 + 22$; weight: $P < 0.001$, $N = 16 + 15$; condition indices: $P < 0.02$, $N = 16 + 15$, Mann-Whitney U-tests); (ii) in females, egg mass correlated positively with body mass ($r = 0.76$, $P \leq 0.01$, $N = 10$). However, the expectation of a higher quality of new than old mates was not supported; in PAE, in three cases weights and condition indices of new partners were higher (2 males, 1 female) and in two cases lower (2 females) following divorce.

Did the initiator of divorce get a partner of higher quality? If the divorce was initiated by one of the two partners this bird should be expected to re-mate first. If old and new partners of the birds that re-mated first were compared, new partners were heavier and had a higher condition index in the two cases where data are available (1 male, 1 female). Following death of a partner, in the three observed cases the new partners were always lighter than their predecessors; in two cases their condition index was lower and in one case it was higher than that of the former mate.

If divorce serves to increase reproductive success, one would expect more chicks to be produced after divorce than before it. However, in the season following divorce two females remained unpaired and two had no chicks with their new partners. Of the five females which remained paired with the same mate and therefore may serve as a control, four had equal numbers of hatchlings in two successive years, and a fifth female had one instead of no chick in the second year. Divorced males produced the same number of hatchlings before and after mate change in two cases and a higher number with the new partner in one case. The three males which remained with their partners (controls) produced the same number of hatchlings in successive years.

If divorce enables the initiating partner to reproduce earlier because its new partner is in an advanced repro-

ductive stage, we would expect divorced birds to reproduce at shorter intervals from the previous brood than non-divorced birds. However, the intervals of clutch initiation from one breeding season to the next were on average about 10 months for both groups of kiwi, with similar values for males and females (Mann-Whitney U-test, $P > 0.1$, $U = 15$, $N = 6$ divorced (3 males + 3 females) and 5 non-divorced (3 males + 2 females)).

Discussion

Mating patterns and parental investment

Social monogamy was found in three populations of North Island Brown Kiwi, irrespective of the sex-ratio bias. This was found also in Little *Apteryx owenii* and Great Spotted Kiwi *Apteryx haastii* (Jolly 1990, McLennan 1990), and can hence be regarded as the predominant mating system of kiwi. In WAI, social monogamy was matched by a high degree of genetic monogamy. Genetic parentage analyses using multilocus fingerprinting and enzyme electrophoresis revealed that 13 of 14 chicks from nine pairs were sired by their putative parents, while one chick apparently resulted from an extra-pair copulation (own unpubl. data). The Waitangi data show that in kiwi a monogamous mating system is stable even with a strong surplus of males, and with a large overlap between paired females' territories and the ranges of unpaired males (see Table 2). This suggests that the environmental polygamy hypothesis cannot explain the mating system of kiwi.

Kiwi males should be expected to ensure the sexual fidelity of their partners during the latter's fertile period because of their enormous broodcare investment. Like in many other bird species (Birkhead and Møller 1992), kiwi males may achieve this by mate guarding. In WAI, partners stayed close to each other for an increased proportion of time during the fertile period of females (own unpubl. data), which suggests mate guarding. However, females should be able to produce additional clutches with other males while their partner is incubating, as male mate guarding is then impossible. In WAI, females were observed to lay replacement clutches for their own partners, but not for other males.

A closer look at the costs of parental investment may suggest a reason why kiwi females are strictly monogamous. Egg production is an extremely expensive task for kiwi females (Calder et al. 1978), affording an extra energy expenditure equivalent to about 100% of basal metabolic rate during the period of egg production, which lasts for about 34 days (Taborsky 1994). After laying the second, and in four cases a third or fourth consecutive egg, females did not recover to their pre-laying weights (Taborsky 1994). A regular, serial production of clutches may therefore reduce their residual reproductive value by increasing their mortality risk (e.g.

via a reduced parasite resistance) or by decreasing their future fecundity (e.g. Bennet and Harvey 1988, Stearns 1992). The common view that in birds brood care is the main demanding parental duty (e.g. Davies 1991), probably does not apply to kiwi. In these birds, the production of female gametes is also a major cost, which apparently bears on the mating system (Taborsky and Taborsky 1993).

In the north of New Zealand the average monthly temperatures between July and October (i.e. the four months in which the majority of kiwi in WAI was reproducing) are on average 11, 11, 12 and 14°C, respectively (from data given for Auckland in Tomlinson 1976). On Stewart Island, the average temperatures during these months are on average 5.5 degrees colder, with occasional frosts (calculated from data given for Invercargill in Tomlinson 1976). We think that because of these climatic conditions, females on the North Island are emancipated from incubation, which enables them to produce two egg clutches. On Stewart Island, however, females share in incubation suggesting that males cannot cope with incubation alone. Incubation duties and the cooler temperatures may constrain females to produce only one-egg clutches. In this situation, females probably recover more slowly from reproduction than males, because the costs of incubation add to the high costs of egg production. Therefore, on Stewart Island females are likely limiting the reproductive rate of males who could improve their reproductive success by sequential polygyny. Polygyny may have occurred in one third of the STE mating units.

Comparative data of two other kiwi species support the suggestion that the climate may be of major importance for kiwi reproduction. In Great Spotted Kiwi inhabiting the South Island's west with its cold and moist climate, females share in incubation and produce only one-egg clutches (McLennan 1990, McLennan and McCann 1991a, b). Little Spotted Kiwi inhabiting Kapiti Island with a milder climate off New Zealand's North Island produce one- and two-egg clutches, and only the males incubate (Jolly 1990).

We conclude that the parental limitation hypothesis is much more likely to explain the mating system of kiwi than the environmental polygamy hypothesis. Monogamy prevails probably because females are energetically constrained from mating with additional partners, while the mating patterns vary independently of marked sex-ratio differences between kiwi populations.

The significance of territories

Taborsky and Taborsky (1991) suggested that the prime function of kiwi territoriality may be female retention, because in WAI, males, although smaller than females, were the more strongly territorial sex. Territori-

ality and pair stability co-occurred in WAI, HAW and STE, and also in Little and Great Spotted Kiwi (Jolly 1990, McLennan and McCann 1991a), whereas in the only population without territory defence (PAE) there was also a high divorce rate. This supports the hypothesis of a primarily reproductive function of territoriality in kiwi. A possible reason for the lack of territoriality in PAE is the high abundance of females. If males cannot breed with more than one female at a time because of broodcare limitations (see above), males would gain little from monopolizing mates when there are 1.6 females to each male.

Comparative interspecific evidence supports the argument that residence and territoriality relate to pair stability. From Rowley's (1983) review of pair stability in birds we calculated a divorce rate of 0% in permanently territorial birds (N = 12), but divorce rates of 31% for resident species that are only partly territorial (N = 5), 38% for migratory species (N = 11) and 7.5% for nomads (N = 22; percentages given are medians calculated from Table 15.6, in Rowley 1983).

The variation in pair stability

The high degree of mate fidelity among kiwi populations suggests benefits to stable pair bonds. The only exception was a yearly divorce rate of 50% in PAE. Often, divorce follows brood failure (e.g. Coulson 1966, Mills 1973, Brooke 1978, Harris et al. 1987), sometimes accompanied by a change to a new breeding site (e.g. Ollason and Dunnet 1988). In PAE kiwi, however, divorce occurred independently of whether a pair had produced offspring in the previous breeding season or not (Potter 1989), and reproductive success did not increase in the season following divorce. In the strongly female-biased population of PAE a number of unpaired adult females was always present. Divorce may have been caused by deliberate pairing of a male with an unpaired female when the latter was ready to lay at an earlier date than his own partner, as unpaired females do not need to recover from reproduction. However, the interval between subsequent clutches was equally long in divorced and non-divorced birds of both sexes.

There was no significant difference between old and new partners of divorced kiwi in body mass or condition indices. Those birds that re-paired first may have improved in partner quality, but data were not sufficient to test this. It is unlikely that PAE kiwi changed their partners to improve the quality of their ranges, because areas were not defended and the access to resources did not appear to be restricted by intraspecific competition. In all but one case of re-mating in PAE and WAI the home ranges of the new partners had already largely overlapped before pairing up (Potter 1989, and own obs.).

Alternatively to an adaptive explanation of pair-splitting, divorce may have been forced upon the members

of a pair. Surplus unpaired females in the population may have replaced previous breeding females, which may result in a "chain-reaction" of divorces and re-matings. Discussions about divorce usually focus on adaptive explanations and ignore the possibility of forced divorce (e.g. Coulson 1966, Rowley 1983, Diamond 1987; but see Black 1996). However, forced divorce appears to be widespread. For example, by far the most divorces observed in Oystercatchers *Haematopus ostralegus* on Schiermonnikoog (Ens et al. 1993: Table I) and in Blue Ducks *Hymenolaimus malacorhynchos* at Manganuiateao River, New Zealand (Williams and McKinney 1996) resulted from forced divorce through usurpation of territories.

Why did forced divorce not occur in the male-biased population of WAI? Unpaired males were lighter and had a lower condition index than paired males (Taborsky and Taborsky 1992). Hence, it is likely that these males were not able to expel territory owners to obtain a partner. However, they were able to fill vacancies generated by the deaths of kiwi in WAI due to dog predation (Taborsky 1988). One unpaired territorial male and one floater male each paired up with widowed females. Additionally, one subadult, previously unpaired female settled in the territory of a widowed male.

In conclusion, we regard it as likely that divorce in kiwi occurs rather as a salvage strategy and not to obtain a mate of higher quality, because (i) there is no evidence for mate improvement after divorce, and (ii) divorce only occurred in a strongly female-biased population, where males do not invest in mate retention by territorial behaviour.

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