Journal of Applied Ecology 2005
42, 91–98

Indirect negative impacts of radio-collaring: sex ratio variation in water voles

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Summary

1. Radio-tracking is used ubiquitously in studies of wild vertebrates, a fundamental assumption being that tagged animals do not significantly differ, behaviourally or otherwise, from untagged animals.
2. We studied two populations of water voles *Arvicola terrestris*: one population was live-trapped from April to September for 2 years (2000, 2001) and then concurrently radio-tracked and trapped in a third year (2002). The second population was trapped only during 2002.
3. During 2002, a substantial decline in female numbers in the radio-collared population was recorded, apparently resulting from a male skew in the sex ratios of offspring born to this population. The mean numbers of males and females born during *trapping* only were 25·7 (SD 2·1) and 29·0 (SD 7·0), respectively. Recruits to the *radio-tracked* population were skewed heavily in favour of males (43 : 13).
4. Both hypotheses commonly invoked to explain mammalian sex-ratio manipulation refer to the condition of mothers. The altered sex ratio resulted from a 48% decrease in numbers of females born, a decrease similar to the proportion (0·49) of the female population that was collared. No similar decline in male births occurred. This suggests that radio-collaring of females caused male-skewed sex ratios.
5. *Synthesis and applications*. We conclude that the observed decline in female numbers resulted from male-skewed recruitment sex ratios due to the attachment of radio-collars to female water voles. These results question the assumption that the use of radio-collars does not fundamentally affect the biology of collared water voles.

Key-words: adverse effects, *Arvicola terrestris*, female recruitment, radio-collars, radio-telemetry, sex ratio

Journal of Applied Ecology (2005) **42**, 91–98
doi: 10.1111/j.1365-2664.2005.00998.x

Introduction

Radio-tracking is ubiquitous in field studies of wild vertebrates. An important assumption is that the behaviour of tagged individuals is representative of those in the population at large. This issue, and the concern that the welfare of the subjects should not be compromised, have been emphasized since the technique's inception in the 1960s (Amlaner & Macdonald 1980), remain as priorities today (Kenward 2001; Withey, Bloxton & Marzluff 2001) and are common to many studies involving the marking of vertebrate species (May 2004).

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Radio-tracking may adversely affect animal populations. Withey, Bloxton & Marzluff (2001) reviewed 96 articles assessing the effects of radio-transmitters on animals. Of these, 47% reported an adverse effect, including effects on reproduction (Ramakka 1972; Cotter & Gratto 1995), weight (Perry 1981; Reynolds 1992; Tuyttens, Macdonald & Raddam 2002), condition (Greenwood & Sargeant 1973; Perry 1981; Jackson, Jackson & Seitz 1985), behaviour (Ramakka 1972; Cotter & Gratto 1995) and survivorship (Webster & Brooks 1980; Werner & Etter 1983). Such impacts could have profound consequences, and some discussion of them has been controversial (Burrows, Hofer & East 1994, 1995 vs. Ginsberg *et al*. 1995; Woodroffe 1997). Tuyttens, Macdonald & Raddam (2003) argued that the effects of tagging may be subtle and important, although difficult to detect.

Water voles *Arvicola terrestris* (Lacepede) are endangered in the UK (Woodroffe, Lawton & Davidson 1990; Macdonald & Strachan 1999; Macdonald & Harrington 2003). We therefore set out to study the population dynamics, dispersion and movement patterns of water voles in two contrasting populations to gain information relevant to their conservation and preservation. We employed radio-tracking amongst other methods.

Several studies of rodent populations, including water voles (Leuze 1976, 1980), have reported no direct impacts of radio-collaring (Smith 1980; Ormiston 1985; Reynolds 1992; Berteaux *et al*. 1996; Johannesen, Andreassen & Steen 1997; de Mendonca 1999). In our study, however, we observed a rapid decline in the number of females present in one of our populations. This led us to consider the possibility that radio-tracking influenced the number of females at this site, potentially by affecting natal sex ratios.

Sex ratio variation is commonly observed as a consequence of varying survival and value of offspring of different sexes. Evolutionary theory suggests that parental investment may favour the sex expected to produce the most grandchildren per unit investment, where this investment influences the fitness of one sex more than the other.

Female condition is an important determinant of natal sex ratios. The local resource competition hypothesis predicts that mothers with access to poor resources should produce offspring of the sex that is most likely to disperse, in order to reduce competition for resources in the natal range (Clark 1978; Silk 1983). Similarly, Trivers & Willard (1973) proposed that the optimal reproductive strategy for a mother is to produce offspring of the sex that can benefit most from the level of resources that she can provide. Both models connect offspring sex ratio with the availability of food resources, expressed through maternal condition.

There is evidence of natal sex ratio variation among water voles. Bazhan, Makarova & Yakovleva (1996) showed that food deprivation during pregnancy almost halved the number of weaned young produced by captive female water voles, and litter sex ratios were skewed in favour of males by > 2 : 1. They also demonstrated increased levels of corticosterone in food-deprived females, suggesting a stress response. Nazarova & Evsikov (2000) demonstrated that captive female water voles gaining relatively little weight during pregnancy weaned smaller, male-biased litters compared with females that gained more weight.

Our aim was to identify the causes of a decline in numbers of female water voles, which was observed in a population that we were radio-tracking, by analysing survival rates, recruitment rates and offspring sex ratios. Our analysis revealed that the most likely cause for the female decline was a shift in the sex ratio of young raised by radio-collared females. This result has implications for conservation research, especially for the monitoring of water vole populations.

Methods

STUDY SITES

The study was conducted at two sites, the Bure Marshes National Nature Reserve (NNR), Norfolk, UK, and the Little Bedwyn stretch of the Kennet and Avon Canal, Wiltshire, UK.

The Bure Marshes NNR (UK grid reference TG 335 165) is a fenland habitat comprising a network of ditches in which water voles hold territories. Within the study area, we deployed live traps (Sherman XLK; $8 \times 9 \times 30$ cm; H.B. Sherman Traps, Inc., Tallahassee, FL, USA) along 4·07 km of ditch edge. The population was open to immigration and emigration in that occupied ditches were accessible from three sides of the site. This site was trapped from April to September in 2000 and 2002 and during April 2003. Public health restrictions, owing to an outbreak of foot and mouth disease, prevented us from trapping between April 2001 and June 2001.

The Little Bedwyn site (UK grid reference SU 295 665) comprises a length of canal running parallel to the River Dun, separated from it by a mown field varying between 20 and 60 m in width. Live traps were deployed along 1·04 km of the canal and 0·96 km of the river, making a total trapped length of 2·0 km. The site was linked to further patches of suitable habitat via the river, and therefore open to dispersal. The Little Bedwyn site was trapped from June 2002 until July 2003.

LIVE-TRAPPING PROTOCOL

Traps were positioned 20 m apart and their positions recorded with a 10-figure grid reference using a global positioning system (GPS Garmin 'Etrex', Garmin Ltd, Romsey, Hants, UK) to a maximum error of 10 m. Traps were baited with apple and contained approximately 150 g of carrot as an overnight food source (*sensu* Efford 1985).

During 2000, half of the Bure Marshes site was trapped in alternate months. During 2001 and 2002, the entire site was trapped each month. Traps were open for four consecutive trap nights per trapping session in 2000 and 2001, and for five consecutive trap nights in 2002. The entire Little Bedwyn site was trapped with one session per month of five trap nights during 2002.

COLLARING PROTOCOL

The radio-collars (TW-4 transmitter, Ag386 cell; Biotrack Ltd, Wareham, Dorset, UK) weighed 4·5 g and were attached only to water voles weighing more than 180 g, representing less than 2·5% of the individual body weight. The collars were of a type commonly used for small mammal monitoring in the UK, comprising a small transmitter and battery imbedded in dental acrylic and fastened in place with a cable tie, trimmed to prevent post-release tightening. The collars had no sharp edges, all joins between components were smoothed and no signs of neck abrasion were found on any animals from which collars were later removed. The collars did not restrict the head movements of the voles.

Handling during collaring took approximately 2 min, did not require anaesthesia and individuals were released immediately at their site of capture. Each animal was fitted only once with a radio-collar, which was removed at the end of the study period.

Water voles were collared only at the Bure Marshes site. Collars were first attached in the last trapping session of the 2001 field season (23 August 2001–7 September 2001). By this time the population had already been live trapped for a total of 9 months over a period of 2 years. Fifteen voles (eight female, seven male) were collared, only one of which survived over-winter (October–March), losing its collar doing so; high over-winter mortality rates are characteristic of the species (Macdonald & Strachan 1999). Water voles were collared throughout 2002 from 17 April until 27 August in an attempt to ensure that eight males and eight females were collared on site at all times. In total, 18 females and 20 males were collared.

RESEARCH DESIGN

Although our original aim was a comparison between two sites, the emerging results led us to consider the hypothesis that the attachment of radio-collars to individuals at the Bure Marshes site resulted in a decline in female numbers attributable to a male bias in the sex ratios of the offspring of collared females. This design was necessarily unreplicated, and followed the form of a before–after control impact pairs (BACIP) design (Stewart-Oaten, Bence & Osenberg 1992). This design determines if a perturbed system differs significantly from what it would have been in the absence of the perturbation: in this case the fitting of radio-collars at the Bure Marshes site.

The before period comprised live trapping at the Bure Marshes site with the absence of radio-collaring in 2000 and 2001. None of the individuals collared at the end of the 2001 field season survived the winter of 2001; the 2002 breeding season, until collaring in late April, was therefore unaffected by previous collaring. The perturbation period comprised live trapping and concurrent radio-collaring from April 2002 onwards at the Bure Marshes site. The control was the live trapping only at the Little Bedwyn site running concurrently with the radio-tracking and trapping at Bure Marshes.

This design departed from a BACIP in that the Little Bedwyn site was not trapped before 2002, making a statistical pair-wise comparison impossible.

Demonstrating that radio-collaring at Bure Marshes precipitated a decline in numbers of female water voles because of an alteration in recruitment sex ratios required that:

1. female, but not male, numbers declined at the Bure Marshes site in 2002 (the perturbation period) and that this did not occur in preceding years (the before period) or at the Little Bedwyn (control) site in 2002;

2. the decline of females in the perturbation period derived from lower female recruitment rates, as opposed to higher female mortality/emigration rates or lower immigration rates;

3. the proportion of the breeding female population collared at the Bure Marshes sites theoretically could be sufficient to account for the observed decline in female recruitment.

ANALYSIS OF POPULATION SIZE, SURVIVAL AND RECRUITMENT RATES

All analysis of survival and recruitment rates and population size estimates were conducted using the program MARK (White & Burnham 1999). Each sex and site was analysed separately. Survival rates and population sizes were estimated using a robust design (Kendall & Nichols 1995; Kendall, Nichols & Hines 1997; Kendall 1999) and recruitment rates of each gender were estimated using Pradel's model for survival and recruitment estimation (Pradel 1996). The estimated number of voles recruited in each session was calculated by multiplying the recruitment rates (numbers of new animals captured at time $t = 2$ per extant member of the population at $t = 1$) by the population estimate from the previous trapping session.

Intervals between trapping sessions were called the primary sampling periods (*sensu* Kendall & Nichols 1995; Kendall, Nichols & Hines 1997), hereafter termed primary periods, in which gains to and losses from the population could occur.

MODEL OF FEMALE RECRUITMENT RATES VS. PROPORTION COLLARED

We present a model of numbers of females at the Bure Marshes site based upon the MARK recruitment rate and survival rate estimates, showing that if theoretically 'sustainable' levels of female recruitment to the Bure Marshes population were reduced by the proportion of the female population collared, this leads to a decline in female numbers similar to that recorded. The model assumes that:

1. collared females would produce only male offspring;

2. the ratio between recruitment rates for each primary period would stay the same if more females were recruited in previous sessions;

3. survival rates of females would be unaffected by increased birth rates of juvenile females.

Not meeting the first assumption would decrease the expected male-biased shift in sex ratio for each collared female and we would find increasingly less correlation between numbers of females collared and female recruitment rates.

The second assumption is reasonable as the relative difference between female recruitment rates in each session during 2002 was similar to that of the male Bure Marshes recruitment rates and female and male recruitment rates at Little Bedwyn during this period (see the Results). The third assumption is reasonable if juvenile female survival rates are similar to those of adults after entering the trapped population. No data exist to support or refute this assumption.

When calculating the actual proportion of the breeding female population that was collared, females weighing more than 140 g were assumed to be of breeding weight; following Stoddart (1971), nearly all captured females above this weight had perforate vaginas.

How the exact proportion of collared voles in each capture session would affect the recruitment for the next month was unknown. The collared proportion was therefore averaged across all capture sessions, simplifying the model and removing this source of uncertainty.

Results

FATES OF COLLARED ANIMALS IN 2002

Nine females slipped collars or died within a week of being collared. Of these, five were definitely taken by predators, three were probably preyed upon (they were never recaptured) and one slipped its collar, remaining alive. Seven male voles slipped collars or died within a week of collaring. Of these, four collars were slipped, one individual was definitely taken by predators and two others were probably preyed upon. For voles that retained a collar for more than 1 week, the mean time spent collared was 69 days for females (n = 9, SD 33, range 20–119) and 76 days for males (n = 13, SD 45, range 22–161).

POPULATION ESTIMATES AND THE FEMALE DECLINE

Whereas the robust design population estimates for both sexes for the Bure Marshes and Little Bedwyn sites were stable during live trapping-only periods (the before and control periods), the numbers of females in the Bure Marshes site declined throughout 2002 (perturbation), reaching a minimum of five in April 2003 (Fig. 1). Female numbers at the Bure Marshes site declined steadily during April to September 2002, from 20 to nine, except for an estimated increase from 13 to 15 from June to July. In contrast, between April and September 2002 the estimated number of males increased from 28 to 35.

SURVIVAL RATES

Survival rates were higher for females than for males at the Bure Marshes site from the outset of the perturbation period (April 2002 onwards) and higher than the survival rates of either sex at Little Bedwyn up to August–September (Fig. 2). The decline in numbers of females at Bure Marshes therefore occurred while their survival rates were the highest of either sex or population.

The best fitting model that estimated survival rates did not incorporate emigration. We therefore excluded the possibility that the female decline at the Bure Marshes derived from unacknowledged emigration because any emigration of females would lower the survival probabilities. Rather, the observed decline must have resulted from low recruitment rates of females into the population.

RECRUITMENT

The MARK estimates for the number of recruits for any site or sex in a given month were within three individuals of the number of new animals captured in all cases, suggesting that the MARK estimates were a good representation of the data.

After April–May 2002 (the perturbation period), the number of females recruited to the Bure Marshes site was consistently lower than during the before period or during any trapping session at Little Bedwyn (the control site; Fig. 3).

At the Bure Marshes site, 51 females and 45 males were recruited during April–September 2000, and 19 females and 15 males from June to September 2001 (the before period). At Little Bedwyn (the control site), 27 females and 46 males were recruited from June to September 2002. During the same period at the Bure Marshes site (June–September 2002; the perturbation

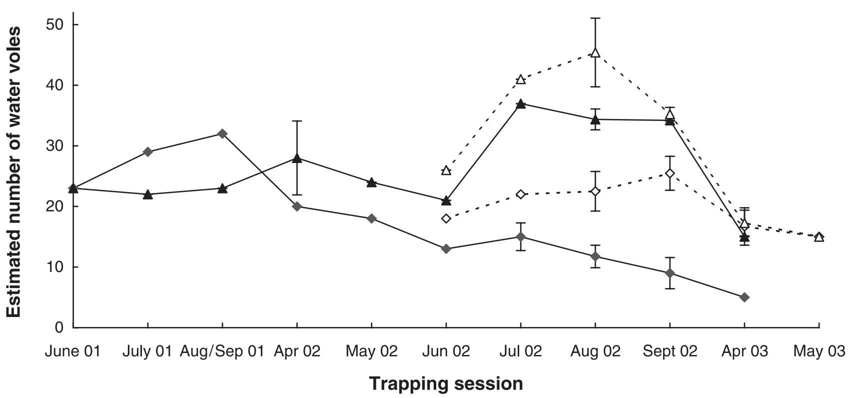

Fig. 1. Estimated population sizes for water voles from 2001 to 2003 at Bure Marshes and Little Bedwyn, UK. Solid lines represent Bure Marshes populations, dotted lines represent Little Bedwyn populations. Triangular points represent males, rhomboid points represent females. Error bars represent SE of population estimate.

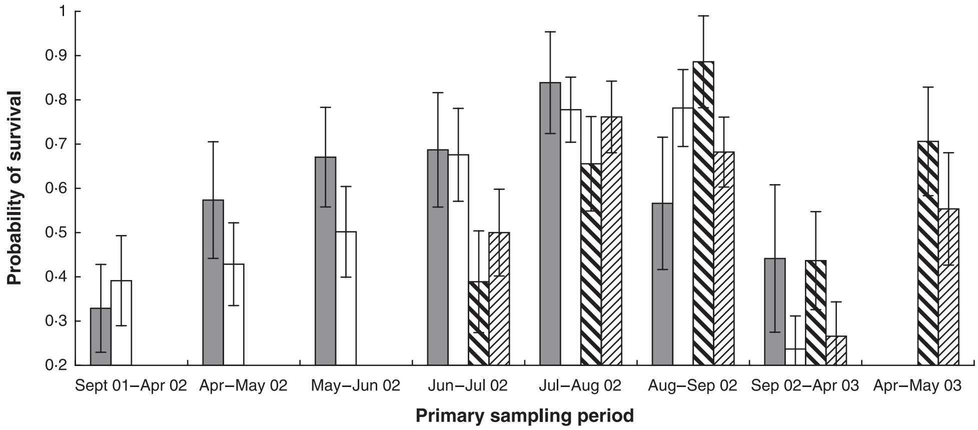

Fig. 2. Survival rates for water voles during primary sampling periods from 2001 to 2003 at Bure Marshes and Little Bedwyn, UK. Solid bars represent Bure Marshes populations, hashed bars represent Little Bedwyn populations. Light bars represent males, dark bars represent females. Error bars represent SE of survival estimate.

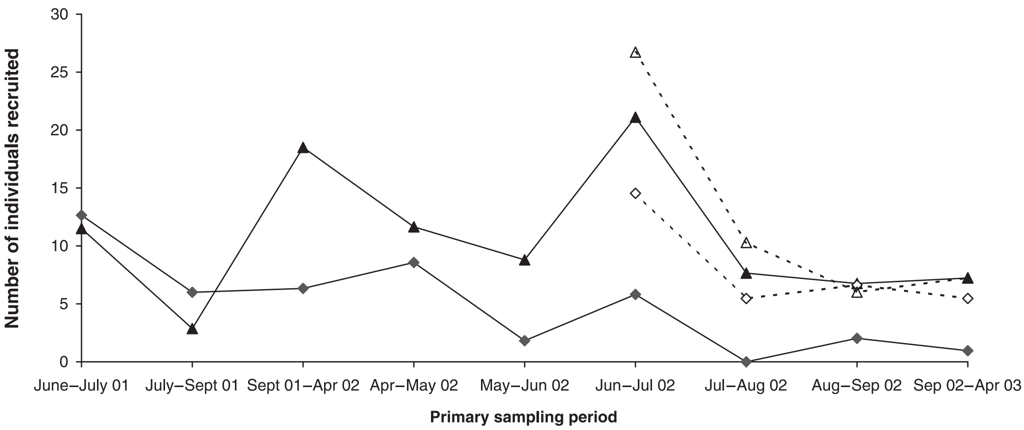

Fig. 3. Estimated numbers of male and female water voles recruited during each primary sampling period between 2001 and 2003 at Bure Marshes and Little Bedwyn. Solid lines represent Bure Marshes populations, dotted lines represent Little Bedwyn populations. Triangular points represent males, rhomboid points represent females. Error bars omitted for clarity.

period), 35 males but only eight females were recruited into the Bure Marshes population. Recruitment sex ratios at Bure Marshes had a male sex bias in 2002 (perturbation period) compared with 2001 ($\chi^2 = 13{\cdot}18$, d.f. = 1, $P < 0{\cdot}001$).

IMMIGRATION AND EMIGRATION RATES

Some recruits in any trapping session could be immigrants from outside the trapped area. Dispersal rates of females at the Bure Marshes site were relatively low, only being detected in approximately 9% of the female population over 2 years. No radio-collared female moved beyond the trapped area of the site during 2002. From the trapping data, only eight females were recorded as moving over 100 m (mean female weekly trapping-derived range for all years 51·8 m), of which only five could be classed as true dispersal (*sensu* Stenseth & Lidicker 1992; Clobert *et al*. 2000). Similarly, for the 2001 season, only four females moved distances greater than 100 m, of which only one could be defined as dispersal.

It is unlikely that a substantial proportion of female recruits to the Bure Marshes population comprised immigrants, and therefore unlikely that the female decline could have derived from reduced immigration rates.

MODELLING THE EFFECTS OF THE PROPORTION OF THE FEMALE POPULATION COLLARED

A mean proportion of 0·49 (SD 0·10) of females above breeding weight at the Bure Marshes site were fitted with collars by the end of each collaring session (Table 1). Numbers of females reconstructed from the survival rate and recruitment rate estimates from the MARK analysis at the Bure Marshes site during the perturbation period agreed closely with actual numbers of females recorded (Table 2a). The largest discrepancy between observed and reconstructed numbers was three individuals in April 2002.

Table 2a represents 'non-sustainable' levels of recruitment into the female Bure Marshes population, in that while the survival rates were the highest of any group (Fig. 2), the recruitment rates were such that the female population declined from 32 to nine between September 2001 and September 2002. Theoretically 'sustainable'

Table 1. The number and proportion of female water voles above breeding weight (140 g) fitted with radio-collars at the end of each capture session

	2001	2002					
Capture session	September	April	May	June	July	August	September
Number of female voles (robust estimate)	32	20	18	13	15	12	9
Number above breeding weight (trapping data)	23	13	15	12	11	8	4
Number collared	8	6	8	8	6	3	2
Proportion above breeding weight collared	0·35	0·46	0·53	0·66	0·38	0·50	0·54

Table 2. Reconstructed numbers of females from the robust design survival estimates and the Pradel recruitment rates, (a) showing the female decline, (b) showing sustainable female recruitment, such that the population remains constant between September 2001 and September 2002, and (c) showing the effects of reducing the sustainable recruitment rates in (b) by the proportion of collared females

	2001	2002						2003
Session	Sep	Apr	May	Jun	Jul	Aug	Sep	Apr
(a)								
Actual numbers	32	20	18	13	15	12	9	5
Estimated numbers	32	16·9	16·9	13·0	14·8	12·4	9·2	5·0
Number survived		10·5	9·7	11·3	9·0	12·4	7·0	4·0
Number recruited		6·3	7·2	1·7	5·8	0·0	2·1	1·0
(b)								
Actual numbers	32	20	18	13	15	12	9	5
Estimated numbers	32	22·7	31·7	27·5	42·5	35·6	32·0	20·7
Number survived		10·5	13·0	21·3	18·9	35·6	20·2	14·1
Number recruited		12·2	18·7	6·2	23·6	0·0	11·8	6·6
(c)								
Actual numbers	32	20	18	13	15	12	9	5
Estimated numbers	32	16·7	16·6	12·8	14·4	12·1	8·9	4·9
Number survived		10·5	9·6	11·2	8·8	12·1	6·8	3·9
Number recruited		6·2	7·0	1·7	5·6	0·0	2·0	0·9

levels of recruitment, in which numbers of females are equal in September 2001 and September 2002, were derived by maintaining the same survival rates but multiplying the recruitment rates by 1·923 (Table 2b). This implies that a sustainable female recruitment rate would have had to be nearly halved (proportionally reduced by [1 – (1/1·923) =] 0·48) to have resulted in the observed decline in the female Bure Marshes population.

The female recruitment rates in the sustainable model (Table 2b) were in the range 0·00–0·86 and similar to those measured at the other sites. Rates for Bedwyn females ranged from 0·21 to 0·81, Bedwyn males from 0·13 to 1·03 and Bure males from 0·21 to 1·01, over the same periods.

Proportionally reducing the theoretically sustainable female recruitment rates in Table 2b by 0·49 (the proportion of females collared; Table 1), results in a decline similar to that recorded at the Bure Marshes (Table 2c), suggesting that the proportion of females collared could have been sufficient to lead to the observed female decline.

Discussion

There was a strong correlation between the radio-collaring of water voles at Bure Marshes and the decline in numbers of females at this site. The decline occurred only during the perturbation period, when voles were being simultaneously radio-collared and live trapped. During this period, the ratio of males to females recruited was 4·8 : 1. No such decline occurred at the Little Bedwyn (control) site, where recruitment sex ratios were 1·6 : 1, or during the 2 previous years of live trapping at Bure Marshes (the before period), during both of which more females were recruited than males (recruitment ratios 1 : 1·1 and 1 : 1·3, respectively). This indicates a dramatic skew in the recruitment sex ratios at Bure Marshes during the perturbation period, which was unlikely to have resulted from either trapping or annual variation but which correlated with the onset of radio-collaring.

The perturbation decline in female numbers was unlikely to have been derived from lowered female survival rates (Fig. 2) or increased emigration rates, but appeared to derive from poor recruitment of juvenile females into the Bure Marshes population. This low recruitment was unlikely to have been caused by a decrease in immigration rates given the low incidence of dispersal recorded in any year at this site.

The model of survival and recruitment rates of females (Table 2a–c) demonstrates that keeping survival rates unaltered but reducing a theoretically stable female recruitment rate by the proportion of the breeding females that are collared was sufficient to account for the perturbation female decline.

We interpret these data to suggest that the 2002 decline in female numbers at the Bure Marshes site resulted from male-skewed offspring sex ratios mediated by a deterioration in maternal condition in response to the attachment of radio-collars to breeding females. Evidence for a detrimental influence of collaring upon small mammals has been shown in a number of studies, including effects upon body mass (Berteaux, Duhamel & Bergeron 1994), activity levels (Berteaux, Duhamel & Bergeron 1994), social interactions (Pouliquen, Leishman & Redhead 1990) and mortality (Wolton & Trowbridge 1985).

In our study there was mortality in the first week following collaring (five confirmed and three suspected cases of predation for females, vs. two and one, respectively, for males). For voles surviving the first week, the mean time spent collared was 69 days for females and 76 days for males. This suggests immediate short-term adverse effects from collar attachment.

Leuze (1980) found no effects of radio-collars upon body weight or fecundity of water voles. Leuze's (1980) collars were of a similar construction to those used in this study, comprising a cable tie attachment with the components embedded in silicone rubber, but they weighed slightly more, at a maximum of 6·1 g, as opposed to 4·5 g. Leuze (1980) recorded only numbers of weanlings seen with the mother, not offspring sex ratios or numbers weaned. Nazarova & Evsikov (2000) showed that low-weight females not only had male-biased litters but a reduced ability to wean offspring successfully. Therefore, Leuze (1980) could have missed alterations in sex ratios or fecundity resulting from collaring.

Skewed sex ratios have been described in stressed and malnourished females of different species (McGinley 1984; Labov *et al*. 1986). Female water voles exhibit decreased litter sizes, male-biased offspring sex ratios and stress responses in response to decreased food availability and body weight (Bazhan, Makarova & Yakovleva 1996; Nazarova & Evsikov 2000).

Female water voles may inherit their mother's territory (Leuze 1976; Strachan 1998), whereas males usually disperse (Leuze 1976). Females inhabiting suboptimal territories may therefore benefit by differentially producing more males (Clark 1978; Silk 1983; Julliard 2000). Radio-collars have the potential to cause stress to water voles: it is possible that such stress might stimulate sex-ratio adjustment as part of an evolutionary mechanism mitigating impacts of suboptimal habitats, similar to the sex-ratio bias and stress response in food-deprived water voles (Bazhan, Makarova & Yakovleva 1996).

Whether the sex ratios in the present study were male skewed from birth or skewed during and post-weaning because of poor female pup survival is unknown. However, in either case the effect would be poor female recruitment and male bias in the juveniles entering the trapped population.

SYNTHESIS AND APPLICATIONS

The implications of this study for further radio-collaring studies of small mammals are likely to be species specific (Withey, Bloxton & Marzluff 2001), and further work is required to establish a causal link between collaring water voles and skew in offspring sex ratios. This study, however, casts doubt on the assumption that the use of radio-collars does not fundamentally affect the biology of collared water voles. This study emphasizes that the effects of commonplace wildlife marking and tracking techniques may be difficult to detect and yet important (Amlaner & Macdonald 1980; May 2004). We recommend caution in the selection of the means used for studying wild populations, especially of rare mammals, and, where possible, additional monitoring for negative impacts upon those populations.

Acknowledgements

We would like to thank the Environment Agency, British Waterways, the People's Trust for Endangered Species and English Nature, who all sponsored this study. Many thanks to our collaborators at Bristol Zoo and Wildwood, Kent, for measuring weights of known-age captive juvenile water voles. We would also like to thank the many volunteers who helped with the fieldwork during this study. Special thanks to Ian Ellis, Rebecca Dean, Gillian McCoy and Ruth Dalton for their help and support during the 2001–3 field season.

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Received 24 August 2004; final copy received 22 November 2004