

Evaluation of short-, mid- and long-term effects of toe clipping on a wild rodent

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Abstract

Context. Toe clipping is a widely used method for permanent marking of small mammals, but its effects are not well known, despite the ethical and scientific implications. Most studies do not find any clear effects, but there is some indication that toe clipping can affect survival in specific cases. Although effects on survival are arguably the most important, more subtle effects are also plausible, yet very few studies have included body condition and none has investigated effects on mobility.

Aims. We analysed the effects of toe clipping on free-living *Mastomys natalensis*, a common, morphologically and behaviourally intermediate small rodent.

Methods. Using a 17-year capture–mark–recapture dataset, we compared movement, body weight and survival between newly and previously clipped animals, and tested whether any of these parameters correlated with the number of clipped toes.

Key results. No evidence for a correlation between total number of clips and any of the variables was found. Newly clipped animals had a slightly smaller weight change and larger travel distance than did those that were already clipped, and we show that this is most likely due to stress caused by being captured, clipped and handled for the first time rather than to the actual clipping.

Conclusions. The combination of trapping, handling and marking has a detectable effect on multimammate mice; however, there is no evidence for a clear effect of toe clipping.

Implications. Our study suggests a re-evaluation of ethical guidelines on small-mammal experiments, so as to reach a rational, fact-based decision on which marking method to use.

Additional keywords: animal ethics, animal welfare, capture–mark–recapture, individual identification, *Mastomys natalensis*, permanent marking, survival.

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Introduction

Many field studies on small mammals need permanently marked animals for individual identification. Several permanent-marking methods exist, each with their own advantages and disadvantages, the choice of which will depend on ethical considerations and the needs and logistical possibilities of the study. Because a marking procedure may affect an animal's behaviour and physiology, care must be taken when extrapolating study results to unmarked animals, which can be done only if the effect of marking has been quantified. So as to make a well informed decision about which marking method to use, it is necessary to have a reliable assessment of the effects of each method. Commonly used identification methods include implanted microchips (PIT-tags), tattooing, ear punching, ear tags, dyes, radio-transmitters and toe clipping (Stockdale 1932; Fullagar and Jewell 1965; Metzgar 1967; Hamley and Falls 1975; Fagerstone and Johns 1987; Ostfeld and Heske 1993; Leclercq and Rozenfeld 2001).

For a thorough overview of animal identification methods, see Murray and Fuller (2000). The main advantages of toe clipping are low costs, short handling times, and the possibility to simultaneously collect tissue samples for genotyping. Disadvantages are the stress and pain suffered by the animal, and possible consequences on survival and behaviour.

Although many institutional welfare guidelines and scientific journals advise against the use of toe clipping and require justification for its use (e.g. National Research Council of the National Academies 2011; Sikes and Gannon 2011), little research has actually been done on the possible effects of toe clipping on small mammals, especially in field studies (Murray and Fuller 2000). Pavone and Boonstra (1985), who investigated the effects of toe clipping on survival by using an unclipped control group and a clipped group of meadow voles, found no effect on body weight, but did observe that toe-clipped males (but not females) had a lower survival in summer. This

interaction between sex and season was attributed to changes in behavioural interactions that occurred only in males. A study by Tamarin and Krebs (1969) found that a combination of blood sampling and toe clipping lowered vole survival in some cases; however, their study design did not allow quantification of the uncombined effects. Owl predation rates and health of *Microtus pennsylvanicus* do not seem to be affected by toe clipping (Fullagar and Jewell 1965; Ambrose 1972). When comparing toe-clipped and PIT-tagged free-living naked mole-rats, Braude and Ciszek (1998) found a slightly lower survival of the latter group, and suggested the use of toe clipping as the most preferable marking technique. The few other studies on small mammal species that exist (see Murray and Fuller 2000) were usually not able to detect any effects of clipping.

The effects of toe clipping are clearly not the same for all small mammals, and in fact the only unambiguous effect found so far is a lower survival on male meadow voles in summer (Pavone and Boonstra 1985). Most existing studies investigated survival, and although this is arguably the most critical effect, it is quite plausible that the consequences are not severe enough to reduce survival probability, but rather assert themselves more subtly, and perhaps only temporarily, as a decrease in mobility and/or lowered body condition. No field studies have looked at mobility, although some indirect evidence for a possible morphological effect has been observed in laboratory studies in the form of decreased suspension-bar grip strength, although this was found in some (Iwaki *et al.* 1989; Schaefer *et al.* 2010), but not all (Castelhano-Carlos *et al.* 2010) studies, and only in newborns. Although laboratory studies have the advantage of a controlled experimental design, their relevance for natural conditions is debatable, and should be followed by evaluations in a field setup (Murray and Fuller 2000).

In this study, we assessed the effect of toe clipping on movement, body condition and survival of the Natal multimammate mouse, *Mastomys natalensis*, a common and widely distributed rodent in Sub-Saharan Africa. *M. natalensis* is a ground-dwelling omnivore, without specialised or exceptional morphological traits and a body size (30–70 g) intermediate for commonly studied small rodents, and can therefore be considered to be a suitable representative for a wide range of small mammal species.

Materials and methods

Trapping and marking

Analyses were conducted using an existing capture–mark–recapture (CMR) dataset. Between March 1994 and January 2011, trapping was conducted monthly for three consecutive nights in a rectangular 300 × 100 m grid of Sherman live traps (76 × 89 × 229 mm, Sherman Live Trap Co., Tallahassee, FL, USA) spaced evenly at 10-m intervals, on the campus of the Sokoine University of Agriculture (Morogoro, Tanzania). This trapping effort resulted in 36 425 captures of 15 471 individuals during 212 700 trap-nights in 223 trapping sessions. At first capture, animals were weighed and sexed, breeding status was determined, and they were marked using a unique toe-clipping code. Because of high abundances (Sluydts *et al.* 2009), combinations of up to six toes per animal were used, with a

maximum of one toe per front paw and two per hind paw. About 2800 unique codes were used in rotation across seasons. A toe was clipped by cutting the upper phalanx with ethanol-cleaned sharp dissection scissors. In 1987, at the start of the CMR studies on rodents in Morogoro, toe clipping was chosen as the marking method because it allows the use of a large number of unique codes, it is easy, fast and cheap to apply and does not use electronic equipment, which at the time was an advantage in Tanzania (Leirs *et al.* 1989). Moreover, the clipped toes provided tissue samples for population genetics research. The same marking technique was used for all follow-up CMR studies in Morogoro. The work was conducted under the animal ethics regulations of Sokoine University of Agriculture and, in retrospect, followed the guidelines in Sikes and Gannon (2011).

The effect of toe clipping was tested with respect to the following four response variables: survival, home range, travel distance and body weight, chosen because they represent relevant ecological traits on different temporal scales. The absence of a proper control group, i.e. non-clipped recaptured individuals, complicated the analyses. Instead, we used an approach in which the four variables were compared between newly and previously marked animals. Because the effect of marking may be confounded by stress caused by being trapped and handled the first time, we also tested for a correlation between the variable of interest and the number of clipped toes, which would indicate a direct effect of toe clipping. Data were divided into the following four classes according to the number of clipped toes: two, three, four, and five/six toes (the latter category pooled because only 18 individuals had six clips).

Survival

Monthly survival was evaluated as a proxy for mid- to long-term clipping effects. The dataset consisted of 223 trapping sessions that were analysed using a standard Cormack–Jolly–Seber approach to survival analysis (Lebreton *et al.* 1992). Because this dataset was too large for the available computational power, it was divided into two subsets, the first containing Sessions 1–111, and the second Sessions 112–223. A goodness-of-fit (GOF) test was conducted to evaluate possible confounding factors such as trap-dependence and an excess of transient animals (Pradel *et al.* 2003). Model selection was based on the AICc (Burnham and Anderson 2002), and the effect of toe clipping was evaluated by comparing the fit of models, including and excluding the effect of clipping in survival and recapture probability.

Home range

Long-term effects were assessed by testing whether home range size correlated with the number of clipped toes. Home range estimation was performed as described in Borremans *et al.* (2014). Briefly, home ranges (using the definition of Burt 1943) were estimated using the minimum convex polygon (MCP) method based on all capture locations, with an inclusive 5-m boundary strip (Stickel 1954). Only animals that were trapped in at least two different months were used for MCP estimation, because these animals were assumed to be resident. To account for an edge effect on MCP size, home ranges with a centroid less than 12 m from the trapping grid edge were removed

from the dataset (Dice 1938; Stickel 1954; Borremans *et al.* 2014). We tested for a correlation between home range size and number of clipped toes, and for an effect of the presence/absence of two clipped toes on the same hind paw by using ANOVA of a linear model including these variables as well as sex and number of recaptures.

Travel distance and weight change

Short- and mid-term effects were investigated through the use of travel distance and weight change between captures. Each time an animal was captured on two consecutive days or months, weight change (body weight at the second capture divided by that at the first, multiplied by 100 to obtain a percentage value) and distance between the two trap locations were calculated. These variables were compared between newly and previously clipped animals, taking into account weight and temporal or environmental effects in the linear mixed model by adding body weight category (10 g interval categories: 0–10 g, 10–20 g, . . . , up to 90 g) and period of the year (January–March, April–June, July–September, October–December) as random effects, and sex and reproductive status as fixed effects. Using the same model variables, we tested for an effect of having two clipped toes on a hind paw and for a correlation with the total number of clipped toes. Models including and excluding variables of interest were compared using likelihood ratio testing. Pregnant females were excluded because sudden weight loss as a result of birth could influence results.

Software

Most data manipulation, statistical analyses and plotting were performed using R (R Core Team 2013), with functions available in R packages RMark 2.1.6-1 (Laake 2013), adehabitatHR (Calenge 2006), gplcib (Peng and Murta 2012), maptools (Lewin-Koh and Bivand 2012), lme4 (Bates *et al.* 2012), matrix (Bates and Maechler 2012) and plotrix (Lemon 2006). U-Care v 2.3.2 was used for GOF calculations (Choquet *et al.* 2009). Error margins denote standard errors unless stated otherwise. Statistical significance was assumed for *P*-values lower than 0.05.

Results

Survival

The global GOF test indicated a strong effect of both an excess of transient animals ($N(0,1) = 8.55$, d.f. = 896, $P < 0.001$) and ‘trap-happiness’ ($N(0,1) = -18.02$, d.f. = 896, $P < 0.001$). These confounding effects were therefore taken into account using the methodology described in Pradel (1993) and Pradel *et al.* (1997). Following the notation in Lebreton *et al.* (1992), we compared the following five models: $\Phi_{(a2+toe)}P_{(m+toe)}$, $\Phi_{(a2+trend)}P_{(m+toe)}$, $\Phi_{(a2)}P_{(m+toe)}$, $\Phi_{(a2+toe)}P_{(m)}$ and $\Phi_{(a2)}P_{(m)}$ (shown in Tables S1 and

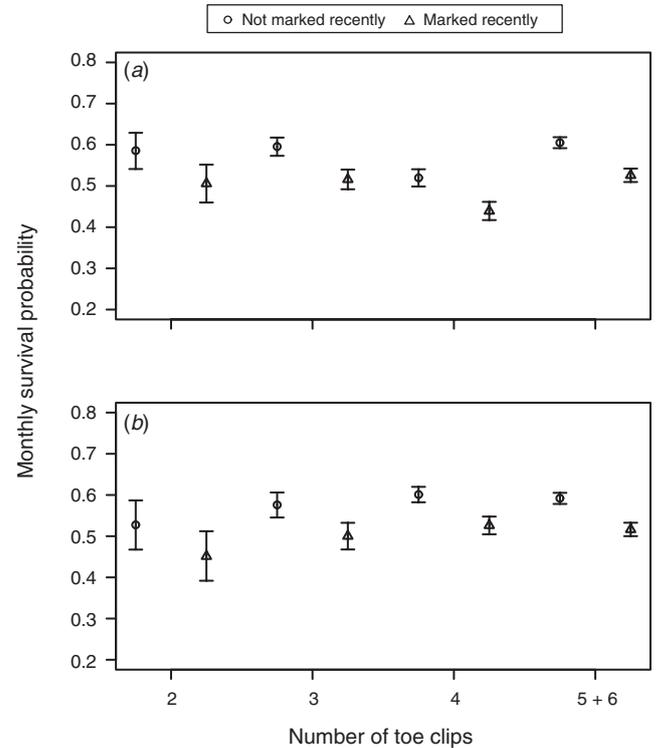


Fig. 1. Survival probability (point estimates with 95% confidence intervals) versus number of clipped toes (mean ± s.e.), for (a) the first and (b) second half of the dataset.

Table 1. Travel-distance statistics

Test statistics of likelihood ratio tests of linear mixed models, testing the effect of different variables on travel distance. Effect estimates (Est) are shown with standard errors (s.e.). Variables are clipping category (newly or previously clipped), sex, reproductive status (juvenile or adult), number of clips (two, three, four or five/six) and the maximum number of hind paw clips (none, one or two). The latter two variables were tested for newly clipped individuals. Statistics for the variable hind clips are the same for both levels (one and two), but effect estimates were estimated for each level

Variable	Travel distance – 1 day					Travel distance – 1 month				
	Est (m)	s.e. (m)	χ^2	d.f.	<i>P</i>	Est (m)	s.e. (m)	χ^2	d.f.	<i>P</i>
Intercept	12.2	3.6	–	–	–	21.8	5.2	–	–	–
Newly clipped	1.9	0.5	15.1	1	<0.001	1.1	0.6	3.63	1	0.057
Male	0.5	0.5	1.27	1	0.26	1.5	0.7	4.76	1	0.029
Juvenile	–2.9	0.7	16.3	1	<0.001	–1.4	1	2.03	1	0.15
Newly clipped × Male	1.3	1	1.79	1	0.18	–0.3	1.2	0.09	1	0.77
Newly clipped × Juvenile	–0.03	1.3	0	1	0.97	2.9	1.6	3.15	1	0.076
Number of clips	1.6	0.9	3.39	1	0.065	–0.01	0.87	0	1	0.99
Hindclips (1)	2.9	6.5	2.62	2	0.27	–5.8	6.1	1.14	2	0.56
Hindclips (2)	0.5	6.8	2.62	2	0.27	–5.2	6.4	1.14	2	0.56

S2, available as Supplementary Material for this paper). Both datasets supported a model including an effect of clipped toes in both survival and recapture probability (Tables S1, S2), but there were no obvious linear trends (Fig. 1, Figs S1, S2, available as Supplementary Material for this paper). Given the confounding effect of transients and the fact that the proportion of transients is higher in the newly clipped category, survival estimates in this category are lower than those of the previously marked group. In the first dataset, the survival estimates for the category of four clipped toes were lower, whereas this was not the case in the second dataset. The most likely reason for this drop appeared to be that, in the first dataset, most individuals with four clips were concentrated in the annual period of population decrease that occurs in the late dry season (Leirs 1994), which was not the case in the second dataset.

Home range

There was no significant correlation between an animal’s number of clipped toes and its home range size ($F=0.08$, $d.f. = 1,4164$, $P=0.78$), and there was no significant interaction between sex and number of toe clips ($F=0.25$, $d.f. = 1,4164$, $P=0.61$). Mean home range sizes per toe-clip category were $637 \pm 48 \text{ m}^2$ (two clips), $680 \pm 30 \text{ m}^2$ (three clips), $626 \pm 21 \text{ m}^2$ (four clips) and $651 \pm 16 \text{ m}^2$ (five/six clips).

Travel distance and weight change

One-day travel distance was higher for newly clipped animals ($13.5 \pm 0.4 \text{ m}$) than for previously clipped animals ($11.9 \pm 0.2 \text{ m}$), but this difference disappeared for 1-month travel distance ($18.6 \pm 0.4 \text{ m}$ and $18.1 \pm 0.4 \text{ m}$ for newly and previously clipped animals, respectively; Table 1). Adults had a larger 1-day, but not 1-month, travel distance than did juveniles, whereas males had a larger 1-month, but not 1-day, travel distance than did females. There were no interactions between clipping category and sex or reproductive status. For newly clipped animals, travel distance was unaffected by the total number of toe clips or the number of hind-paw clips (Fig. 2a).

One-day as well as 1-month weight change were significantly affected by clipping category, sex and reproductive status (Table 2). Newly clipped animals had a lower weight change ($93.5 \pm 0.2\%$ and $102.7 \pm 0.3\%$ 1-day and 1-month weight

change, respectively) than did those that were clipped previously ($94.5 \pm 0.2\%$ and $103.7 \pm 0.3\%$ 1-day and 1-month weight change, respectively); i.e. over 1 day, newly clipped animals lost more weight than did previously clipped animals, whereas over 1 month they gained less weight. Regardless of clipping category, females had a smaller weight change than did males, whereas that of adults was larger than that of juveniles. No correlations were observed between weight change and total number of toe clips or the presence of hind-paw clips (Fig. 2b).

Discussion

Despite our large dataset that should allow the statistical detection of even very small effects, no evidence was found for a correlation between the number of clipped toes and any of

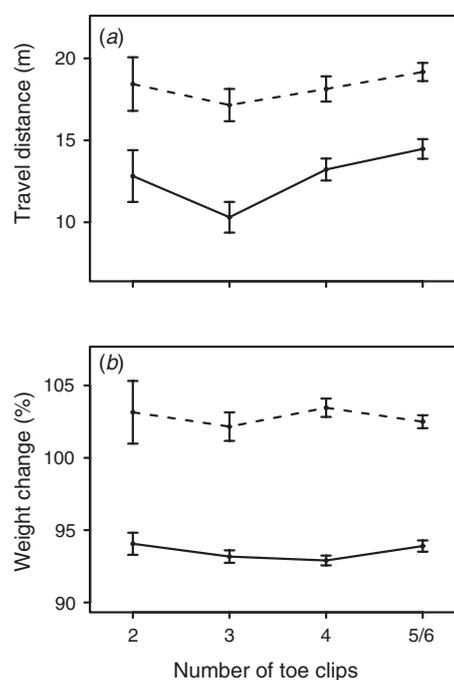


Fig. 2. One-day (full line) and 1-month (dotted line) (a) travel distance and (b) weight change versus number of clipped toes (mean \pm s.e.).

Table 2. Weight-change statistics

Test statistics of likelihood ratio tests of linear mixed models, testing the effect of different variables on travel distance. Effect estimates (Est) are shown with standard errors (s.e.). Variables are clipping category (newly or previously clipped), sex, reproductive status (juvenile or adult), number of clips (two, three, four or five/six) and the maximum number of hind paw clips (none, one or two). The latter two variables were tested for newly clipped individuals. Statistics for the variable hind clips are the same for all levels (one and two), but effect estimates were estimated for each level

Variable	Weight change – 1 day					Weight change – 1 month				
	Est (%)	s.e. (%)	χ^2	d.f.	P	Est (%)	s.e. (%)	χ^2	d.f.	P
Intercept	96.1	2.9	–	–	–	105.5	8.1	–	–	–
Newly clipped	–0.7	0.3	5.62	1	0.018	–3.3	0.5	48.3	1	<0.001
Male	0.8	0.3	6.3	1	0.012	4.2	0.4	102	1	<0.001
Juvenile	–1.1	0.4	6.03	1	0.014	–1.8	0.6	7.44	1	0.006
Newly clipped \times Male	0.5	0.6	0.55	1	0.46	–0.5	0.8	0.39	1	0.53
Newly clipped \times Juvenile	–0.2	0.8	0.03	1	0.86	2.1	1.2	3.3	1	0.069
Number of clips	–0.1	0.6	0.03	1	0.87	–1	0.7	2.04	1	0.15
Hindclips (1)	–2.4	3.9	1.07	2	0.59	2.1	3.9	0.35	2	0.84
Hindclips (2)	–1.7	4.1	1.07	2	0.59	2.4	4.1	0.35	2	0.84

the studied variables. We did observe that newly clipped animals lost more (1 day) or gained less (1 month) body weight than did those that were already clipped. However, these differences were small, being 3.3% in 1 month and 0.7% in 1 day, which, for an animal with a body weight of 30 g, would translate into 0.9 g (3.3%) and 0.21 g (0.7%). So, although statistically significant, the biological significance of this difference is debatable. Movement was affected similarly by recent clipping, resulting in a larger travel distance from the last trap location, but this was the case only for the first day (and not 1 month) after clipping. Because these effects on weight change and movement were small and unaffected by the number of clipped toes, they were not necessarily due to wounding.

Instead, our findings suggested that the observed effects are transient and more likely caused by stress, as a result of being captured and handled for the first time. Similar conclusions were reached by Korn (1987), who investigated the effects of toe clipping on five rodent species and found no biologically relevant effects but did observe small weight losses as a result of trapping-related stress. If true, this means that these effects can be expected regardless of which marking method is used, because they all require stressing and wounding the animal in some way. Indeed, when using ear-tattooing for permanent marking of grey-sided voles, the time interval between the first and the second capture has been observed to be longer than that between consecutive captures (Lindner and Fuelling 2002).

To inform and improve ethical guidelines on animal experiments and field study methods, it is necessary to evaluate the effects of marking methods in a range of settings and for multiple species. Our study on the multimammate mouse, a morphologically and behaviourally intermediate small rodent, found no evidence for any direct effects of toe clipping, but did observe a stress effect most likely caused by being captured and handled for the first time, which disappeared in consecutive captures. This calls into question the current recommendations against the use of toe clipping, and encourages a critical re-evaluation so as to make a rational, fact-based decision on which method to use for the permanent identification of small mammals.

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References

- Ambrose, H. W. (1972). Effect of habitat familiarity and toe-clipping on rate of owl predation in *Microtus pennsylvanicus*. *Journal of Mammalogy* **53**, 909–912. doi:10.2307/1379235
- Bates, D., and Maechler, M. (2012). 'Matrix: Sparse and Dens Matrix Classes and Methods. R package Version 1.0-9.' Available at <http://Matrix.R-forge.R-project.org/> [Verified October 2014]
- Bates, D., Maechler, M., and Bolker, B. (2012). 'lme4: Linear Mixed-effects Models using Eigen and Eigenfunctions. R package Version 0.999999-0.' Available at <http://CRAN.R-project.org/package=lme4>.
- Borremans, B., Hughes, N. K., Reijnen, J., Sluydts, V., Katakweba, A. A. S., Mulungu, L. S., Sabuni, C. A., Makundi, R. H., and Leirs, H. (2014). Happily together forever: temporal variation in spatial patterns and complete lack of territoriality in a promiscuous rodent. *Population Ecology* **56**, 109–118. doi:10.1007/s10144-013-0393-2
- Braude, S., and Cizek, D. (1998). Survival of naked mole-rats marked by implantable transponders and toe-clipping. *Journal of Mammalogy* **79**, 360–363. doi:10.2307/1382873
- Burnham, K. P., and Anderson, D. R. (2002). 'Model Selection and Multimodel Inference: a Practical Information-theoretic Approach.' (Springer: New York.)
- Burt, W. H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* **24**, 346–352. doi:10.2307/1374834
- Calenge, C. (2006). The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* **197**, 516–519. doi:10.1016/j.ecolmodel.2006.03.017
- Castelano-Carlos, M. J., Sousa, N., Ohl, F., and Baumans, V. (2010). Identification methods in newborn C57BL/6 mice: a developmental and behavioural evaluation. *Laboratory Animals* **44**, 88–103. doi:10.1258/la.2009.009044
- Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., and Pradel, R. (2009). U-CARE: utilities for performing goodness of fit tests and manipulating CAPTURE-RECAPTURE data. *Ecography* **32**, 1071–1074. doi:10.1111/j.1600-0587.2009.05968.x
- Dice, L. R. (1938). Some census methods for mammals. *The Journal of Wildlife Management* **2**, 119–130. doi:10.2307/3796432
- Fagerstone, K. A., and Johns, B. A. (1987). Transponders as permanent identification markers for domestic ferrets, black-footed ferrets, and other wildlife. *The Journal of Wildlife Management* **51**, 294–297. doi:10.2307/3801005
- Fullagar, P. J., and Jewell, P. A. (1965). Marking small rodents and the difficulties of using leg rings. *Journal of Zoology* **147**, 224–228. doi:10.1111/j.1469-7998.1965.tb04647.x
- Hamley, J. M., and Falls, J. B. (1975). Reduced activity in transmitter-carrying voles. *Canadian Journal of Zoology* **53**, 1476–1478. doi:10.1139/z75-179
- Iwaki, S., Matsuo, A., and Kast, A. (1989). Identification of newborn rats by tattooing. *Laboratory Animals* **23**, 361–364. doi:10.1258/002367789780746024
- Korn, H. (1987). Effects of live-trapping and toe-clipping on body weight of European and African rodent species. *Oecologia* **71**, 597–600. doi:10.1007/BF00379304
- Laake, J. (2013). RMark: an R interface for analysis of capture-recapture data with MARK. In 'AFSC Processed Report 2013-01'. pp. 25. Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle, WA.
- Lebreton, J., Burnham, K., Clobert, J., and Anderson, D. (1992). Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118. doi:10.2307/2937171
- Leclercq, G. C., and Rozenfeld, F. M. (2001). A permanent marking method to identify individual small rodents from birth to sexual maturity. *Journal of Zoology* **254**, 203–206. doi:10.1017/S0952836901000711
- Leirs, H. (1994). 'Population Ecology of *Mastomys natalensis* (Smith, 1834). Implications for Rodent Control in Africa.' Agricultural Ed. Nr35. (Belgian Administration for Development Cooperation: Brussels.)
- Leirs, H., Verheyen, W., Michiels, M., Verhagen, R., and Stuyck, J. (1989). The relation between rainfall and the breeding season of *Mastomys natalensis* (Smith, 1834) in Morogoro, Tanzania. *Annales de la Societe Royale Zoologique de Belgique* **119**, 59–64.

- Lemon, J. (2006). Plotrix: a package in the red light district of R. *R News* **6**, 8–12.
- Lewin-Koh, N. J., and Bivand, R. (2012). 'Maptools: Tools for Reading and Handling Spatial Objects. R Package Version 0.8-18.' Available at <http://CRAN.R-project.org/package=maptools>.
- Lindner, E., and Fuelling, O. (2002). Marking methods in small mammals: ear-tattoo as an alternative to toe-clipping. *Journal of Zoology* **256**, 159–163. doi:10.1017/S0952836902000195
- Metzgar, L. H. (1967). An experimental comparison of screech owl predation on resident and transient white-footed mice (*Peromyscus leucopus*). *Journal of Mammalogy* **48**, 387–391. doi:10.2307/1377771
- Murray, D., and Fuller, M. (2000). A critical review of the effects of marking on the biology of vertebrates. In 'Research Techniques in Animal Ecology'. (Eds L. Boitani and T. K. Fuller.) pp. 15–64. (Columbia University Press: New York.)
- National Research Council of the National Academies (2011). 'Guide for the Care and Use of Laboratory Animals.' 8th edn. (National Research Council of the National Academies: Washington, DC.)
- Ostfeld, R. S., and Heske, E. J. (1993). Sexual dimorphism and mating systems in voles. *Journal of Mammalogy* **74**, 230–233. doi:10.2307/1381925
- Pavone, L., and Boonstra, R. (1985). The effects of toe clipping on the survival of the meadow vole (*Microtus pennsylvanicus*). *Canadian Journal of Zoology* **63**, 499–501. doi:10.1139/z85-072
- Peng, R. D., and Murta, A. (2012). 'gpclib: General Polygon Clipping Library for R. R Package Version 1.5-3.' Available at <http://CRAN.R-project.org/package=gpclib>.
- Pradel, R. (1993). Flexibility in survival analysis from re-capture data: handling trap-dependence. In 'Marked Individuals in the Study of Bird Population'. (Eds J. Lebreton and P. North.) pp. 29–37. (Birkhäuser: Basel, Switzerland.)
- Pradel, R., Hines, J., Lebreton, J., and Nichols, J. (1997). Capture–recapture survival models taking account of transients. *Biometrics* **53**, 60–72. doi:10.2307/2533097
- Pradel, R., Wintrebert, C., and Gimenez, O. (2003). A proposal for a goodness-of-fit test to the Arnason–Schwarz multisite capture–recapture model. *Biometrics* **59**, 43–53. doi:10.1111/1541-0420.00006
- R Core Team (2013). 'R: a Language and Environment for Statistical Computing.' Available at <http://www.r-project.org>.
- Schaefer, D. C., Asner, I. N., Seifert, B., Bürki, K., and Cinelli, P. (2010). Analysis of physiological and behavioural parameters in mice after toe clipping as newborns. *Laboratory Animals* **44**, 7–13. doi:10.1258/la.2009.009020
- Sikes, R. S., and Gannon, W. L. (2011). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* **92**, 235–253. doi:10.1644/10-MAMM-F-355.1
- Sluydts, V., Davis, S., Mercelis, S., and Leirs, H. (2009). Comparison of multimammate mouse (*Mastomys natalensis*) demography in monoculture and mosaic agricultural habitat: implications for pest management. *Crop Protection* **28**, 647–654. doi:10.1016/j.cropro.2009.03.018
- Stickel, L. F. (1954). A comparison of certain methods of measuring ranges of small mammals. *Journal of Mammalogy* **35**, 1–15. doi:10.2307/1376067
- Stockdale, L. G. (1932). Technique for marking rats numerically with dye. *Journal of Comparative Psychology* **14**, 237–240. doi:10.1037/h0072053
- Tamarin, R., and Krebs, C. (1969). *Microtus* population biology. II. Genetic changes at the transferrin locus in fluctuating populations of two vole species. *Evolution* **23**, 183–211. doi:10.2307/2406785