

Where have all the cavies gone? Causes and consequences of predation by the minor grison on a wild cavy population

Cornelia Kraus and Heiko G. Rödel

Kraus, C. and Rödel, H. G. 2004. Where have all the cavies gone? Causes and consequences of predation by the minor grison on a wild cavy population. – *Oikos* 105: 489–500.

We investigated whether predation by the minor grison (*Galictis cuja*, a small mustelid) played a key role in limiting a wild cavy population (*Cavia magna*), ultimately leading to its local extinction. Radio-telemetry and capture-mark-recapture techniques were used to estimate grison predation rates (kill rates), time-specific probabilities of apparent mortality (population loss rate), overall mortality and grison predation for the cavy population. Additionally, we present data on alternative prey species, grison diet and reproduction to show potential proximate mechanisms of grison predation on wild cavies. The predictions specified were mostly confirmed: (1) grison predation was responsible for almost 80% of the cavies killed by known predators; (2) grison predation probabilities paralleled those of overall mortality of cavies over time; and (3) also those of the apparent mortality of the population. Thus, the population dynamics and the local extinction of the cavy population were not due to emigration processes. (4) Grison predation rates were not density-dependent, but showed pronounced peaks during the austral summer. The grison mainly preyed on small mammals: two water-rat species and the wild cavies. When the availability of alternative prey decreased in summer, the grison appeared to specialise on cavies. The onset of grison reproduction was somewhat delayed in relation to the onset of cavy reproduction. The lack of alternative prey coincided with high grison food demands due to reproduction, leading to a very high predation pressure ultimately resulting in the local extinction of the cavy population. We conclude that grison predation was indeed the main factor driving changes of the cavy population studied and speculate why caviomorph rodents might be especially susceptible to local extinction processes.

C. Kraus, Dept of Animal Behaviour, Univ. of Bielefeld, P.O. Box 100131, DE-335001 Bielefeld, Germany. – H. G. Rödel, Dept of Animal Physiology, Univ. of Bayreuth, Universitätsstrasse 30, DE-95440 Bayreuth, Germany.

The role vertebrate predators play in the limitation of their prey populations varies widely (reviewed by Sinclair 1989, Sinclair and Pech 1996). They may act as a compensatory factor of mortality, removing only doomed surplus individuals (Errington 1946, 1956, ungulates: Skogland 1991, birds: Côté and Sutherland 1997) or as a regulating agent causing stable population equilibria and limit cycles (Rosenzweig and MacArthur 1963, May 1981). In other cases predation can keep a population low, but once the prey density is above a

certain threshold level, predation loses its regulatory power (Pearson 1964, 1966, 1971, Corbett and Newsome 1987, Trout and Titensor 1989, Sinclair et al. 1990, Pech et al. 1992).

How predators affect prey populations depends on many factors. Whereas the functional response of generalist predators tends to stabilise prey numbers by switching among alternative prey species (Anderson and Erlinge 1977, Erlinge et al. 1983, 1984, 1988, Hanski et al. 1991, Lambin et al. 2000), specialists might drive

Accepted 31 October 2003

Copyright © OIKOS 2004
ISSN 0030-1299

predator–prey limit cycles by a delayed density-dependent numerical response (May 1981, Hanski et al. 1991, Royama 1992, Turchin and Ostfeld 1997, Graham and Lambin 2002, Korpimäki et al. 2002). Predation may also cause changes in reproductive parameters of the prey population (Magnhagen 1991, Korpimäki et al. 1994, Karels et al. 2000). Other potential factors include intrinsic growth rates of predator and prey species (Tanner 1975), sex- and/or age-specific predation (Kouvunen et al. 1996, Norrdahl and Korpimäki 1998, Sommer 2000) and behavioural changes of the prey (Cassini 1991, Norrdahl and Korpimäki 1998, Jonsson et al. 2000, Sommer 2000, Ylönen et al. 2002).

Much of our knowledge about the impact of predators on populations of small mammals stems from research on cyclic populations in northern latitudes (reviewed by Hanski 1987, Hansson and Henttonen 1988, Korpimäki and Krebs 1996, Krebs 1996, Hanski et al. 2001, Krebs et al. 2001). Observational (Fitzgerald 1977, Angelstam et al. 1984, Hansson 1984, Henttonen et al. 1987, Korpimäki et al. 1991) and experimental studies (Krebs et al. 1995, Korpimäki and Norrdahl 1998, Klemola et al. 2000, Korpimäki et al. 2002), as well as empirically-based and theoretical models (Hanski et al. 1991, 1993, Akçakaya 1992, Stenseth et al. 1996, Lidicker 2000) suggest that predation, especially by small mustelids, is a key factor driving these population fluctuations. As Hanski et al. (2001) noted, not much is known about the impact of vertebrate predators on populations of small mammals outside Fennoscandia or North America (Jaksić 1986, Jaksić et al. 1992, Meserve et al. 1993, 1996). Studies of predator–prey systems in other regions are needed to test the general validity of these hypotheses.

In this paper we document the local extinction of a population of *Cavia magna* and evaluate the role that predation by a small mustelid, the minor grison (*Galictis cuja*), played in limiting this population. Cavies (Caviidae) are a widely distributed South-American family of medium-sized hystricomorph rodents. Some authors suggest that wild cavy populations show ‘cycles’ or outbreaks (Galante and Cassini 1994). They are also reported to be heavily preyed upon by a large variety of predators (Rood 1972, Jaksić 1986, Cassini 1991, Asher and Sachser 2000). Little is known about the minor grison; it is described as a generalist predator mainly feeding on small mammals (Ebensperger et al. 1991). Diuk-Wasser and Cassini (1998) believe that it is capable of controlling rabbit populations in the southern Neotropics.

Many studies on predation use population density indices obtained from snap trapping (Henttonen et al. 1987, Norrdahl and Korpimäki 1993) or minimum numbers known alive (Boonstra 1977, Meserve et al. 1996) to assess changes in prey and predator populations, thus survival and recapture probabilities are

inevitably confounded. Prey remains in predator faeces are often used to estimate predation rates (Erlinge et al. 1983, Korpimäki et al. 1991) – but these are based on a number of unrealistic assumptions (e.g. independence and randomness of faecal samples and known total amount of faeces produced). In this study we chose a much more direct approach applying radio-telemetry and capture-mark-recapture techniques to estimate predation rates and cavy population parameters.

To investigate the hypothesis that predation by the minor grison was the main factor limiting the cavy population finally leading to its local extinction we tested the following predictions: (1) grison predation was the main cause of mortality in cavies (however, this could also be the case if the grison removed the ‘doomed surplus’ at certain times of the year, e.g. during harsh winter periods); (2) if grison predation had a strong and consistent impact on cavy population dynamics over time, we would additionally expect that the time course of grison predation probabilities closely parallels the overall mortality probabilities of the cavies; (3) overall mortality probabilities and those of grison predation should also parallel apparent mortality probabilities (loss rate of the population; this combines mortality and emigration) of the cavy population to exclude emigration as a key factor in cavy population dynamics; and (4) grison predation rates (number of cavies killed per time interval \neq grison predation probability) are not directly density-dependent; otherwise no local extinction would be possible. Additionally, we discuss data on alternative prey species, grison diet and reproduction in order to elucidate potential proximate mechanisms of the local extinction process.

Methods

Study area and study population

The study site was located within the Refugio de Fauna Laguna de Castillos national park, in the Rocha department of Uruguay near the Atlantic coast. An extensive ‘caraguatal’ (ca 3.3 ha), consisting of a typical wetland vegetation dominated by key species *Eryngium pandanifolium* (a tall spiny shrub) and surrounded by short and long grasses, provided protection and food for co-existing populations of *C. aperea* and *C. magna*. A large variety of potential predators inhabit the area. These include mammalian predators such as *Cerdocyon thous* (Canidae), *Galictis cuja* (Mustelidae) and *Lutreolina crassicaudata* (Felidae), *Lutreolina crassicaudata* (Didelphidae); raptors such as *Circus cinereus*, *C. buffoni*, *Buteo magnirostris* (Accipitridae), *Milvago chimango*, *Polyborus plancus*, (Falconidae) and *Bubo virginianus* (Strigidae), as well as some serpents such as *Philodryas patagoniensis* (Colubridae) that could also potentially prey on wild cavies (see Gambarotta et al.

1999 for a more detailed description of the reserve and its fauna). Due to the humid climate (precipitation: ~ 1100 mm/year) as well as the low altitude (0 m a.s.l.), the area is characterized by marked seasonality with partial flooding occurring during the winter months (March/April to October/November); the duration and extent of flooding varies strongly from year to year. To facilitate fieldwork, a grid system (250 × 200 m) was established with wooden stakes marking the intersections at 10-m distances.

Capture-mark-recapture

From May 1999 to January 2001, we monitored the wild cavy population by a systematic capture-mark-recapture study, utilising 200 live traps (Tomahawk Live Trap, Tomahawk, U.S.) distributed throughout the grid system. The complete 'caraguatal' and parts of the grassland were sampled to ensure that the area covered by traps covered the entire cavy population. Trapping sessions were conducted twice monthly (at approximately fortnightly intervals) for two consecutive nights. As cavy are most active during twilight, traps were left open between four and five hours around sunset and sunrise, and closed for the remainder of the day. Between trapping sessions, traps were inactivated and left open in order to habituate the animals to the traps and to prevent them from changing their preferred paths. When captured for the first time, each individual was fitted with a transponder (Trovan, UK) which was inserted subcutaneously between the shoulders, as well as marked with a numbered ear tag (National Band and Tag Co., U.S.). The sex and reproductive status of each individual was determined and body mass and total length were recorded. Cavy trap occupancy rate often exceeded 20% during the first year (maximum 28%) but stayed well below 10% for the remainder of the study.

In addition to the cavy, we regularly caught other rodent species which we did not mark individually. We used the combined maximum number of individuals of the water-rat species *Holochilus brasiliensis* and *Scapteromys tumidus* caught during any one of the four trapping units of each trapping session as a crude index of abundance of the larger small rodents occurring in the study area. Information on grison reproduction stems from occasional catches and sightings of members of the grison family. We also caught and marked one adult grison female and one sub-adult grison male with transponders and ear tags.

Radio-tracking

In addition to the capture-mark-recapture study, we fitted a total of 55 female and 49 male adult *C. magna* with radio transmitters. These possessed an external

antenna and a life expectancy of 4 months (Sirtrack, New Zealand). The proportion of the trappable population that was fitted with collars ranged between an estimated 2% in the beginning of the study to virtually 100% in September 2000 (average 28%). To minimize the risk of injury, cable tie collars covered with silicon tubing were used to fix the transmitters. The entire set-up weighed between 4 and 6 g, thus representing only 0.6 to 2.0% of the animal's body mass. All radio-collared animals were usually located once to six times a day (receiver: Telonics, U.S., aerial: Sirtrack, New Zealand). The longest time interval during which we did not check for tagged animals was 10 days and thus shorter than the fortnightly time-scale of our data (not of our data analysis, see below).

If an animal did not change its location for more than two days, a search for it was conducted. In case a signal could not be received from the study site, we searched for the animal within a radius of approximately 500 m: the maximum distance at which a dislocated transmitter was found was ~ 1 km. In most cases it was possible to determine the cause of death of the individual due to bite marks, the remains and/or the location of discovery. Grisons generally transferred their prey into their extensive burrow system or left the remains near one of the entrances – consisting of the skull fragmented at the base, as well as skin remains. Raptors left the transmitter on open grass patches, and sometimes the intestines were placed neatly beside them. We were not able to identify the raptor species responsible for a particular kill. Transmitters of fox victims (*Cerdocyon thous*) were also left openly, and apart from fox tracks, usually just some hairs of the cavy remained. In case of transmitter failure we often caught the cavy in a later trapping session and removed or exchanged the radio-collar (8 times).

Diet of the minor grison

Faecal samples of the minor grison were collected during two periods: 15–20 September 1999 (n = 20) and 10–15 January 2001 (n = 49). Nearly all samples were found at entrances of the grisons' burrow system which was situated next to our study site. However, we also discovered a small number of faeces inside the burrow while digging for a radio transmitter of a cavy which had been taken by the grison. As a result of heavy rainfall prior to both collection periods, we assume that the prey remains in the faeces represented the diet composition of the minor grison during the narrow time window of two weeks at most. Faecal samples were air-dried and stored separately in labelled paper bags. In the laboratory, prey hair was identified macroscopically by colour and shape, and microscopically analysis of internal hair structure and external scale patterns following the methods in Teerink (1991) was also carried out.

In order to identify potential prey species which were based on a specimen list for this area (Gambarrotta et al. 1999), we used a reference collection provided by the Universidad de la Republica, Montevideo. For each prey item, the frequency of occurrence (per number of faeces) was calculated. This was done separately for the samples collected during the two periods.

Data analysis

We modelled survival probabilities S (1-mortality probabilities) of radio-collared cavies with the KNOWN FATES option in program MARK (White and Burnham 1999). To obtain estimates of grison predation probability, we right-censored data of all animals that died due to other factors of mortality, analogous to the treatment of unknown fates (Lee 1992). We were mainly interested in the time course of mortality probabilities: local extinction could be due to a sudden rise in mortality (model S_t : = survival variable over time t) or the consequence of a constant 'drain' on the population, if recruitment cannot overcompensate mortality (model S : = constant survival probability). Still, sample sizes were too small to use the fortnightly time intervals (boundary estimates of $S_t = 1$ would be obtained for many of these intervals). As a compromise between useful time intervals and variance, we decided to use three-monthly ('seasonal') intervals. To achieve this, we assumed that the survival rates were constant over this period. The time structure for our models consisted of six three-monthly periods followed by one two-monthly and finally one fortnightly interval. We kept the last two intervals separate because we knew that a strong increase in mortality occurred during these last two weeks; we lost almost all our radio-collared individuals to grison predation within a few days. We also included sex as another factor potentially affecting survival, because predators might prey preferentially on one sex or age, and the sex ratio of our population changed considerably over the course of our study (Kraus et al. 2003). Since we only tagged relatively large adults, we could not include age as a factor.

To compare overall mortality and grison predation probabilities of the radio-tagged cavies to those of apparent mortality ($1 - \phi$ = mortality + permanent emigration, ϕ : = apparent survival) of the whole population, we applied the Cormack-Jolly-Seber model (Cormack 1964, Jolly 1965, Seber 1965, also in program MARK) to our capture-recapture data. As our purpose was not to find the best approximating model for apparent mortality but to obtain estimates comparable to the best approximating model for grison predation (i.e. $S_{s \times t}$), we used models allowing for an interaction between sex and time ($\phi_{s \times t}$). We only modelled recapture probabilities p , which we knew to be highly variable over the

study period ($p_{s \times t}$, p_{s+t} , p_t , where $s+t$ denotes an additive effect of sex and time, i.e. parallel lines on a logit scale). We assessed the goodness-of-fit for the global model ($\phi_{s \times t}$, $p_{s \times t}$) and adjusted model selection statistics and standard errors according to the over-dispersion parameter c , estimated as \hat{c} from the parametric bootstrap procedure available in MARK (1000) simulations, $\hat{c} = 1.055$, $P = 0.206$.

The models' notation follows that of Lebreton et al. (1992). We based model selection on Akaike's information criterion (AIC, Akaike 1973, 1985) as described in Burnham and Anderson (1998). Because our sample sizes were rather small, we used the second-order variant of AIC, the AIC_c . We employed AIC differences ($\Delta_i = AIC_i - \text{minimum AIC}$) to compare the support the different models had of being the estimated best approximating model in the set. According to Burnham and Anderson (1998), models with $\Delta_i \leq 2$ gain substantial support, models having $4 < \Delta_i < 7$ achieve some support, whereas models with $\Delta_i > 10$ have little support, or fail to account for some important explainable variation in the data and hence might be omitted from further consideration. Additionally, we present Akaike weights (w_i) to judge the relative likelihood of competing models.

To understand the proximate mechanisms affecting grison predation on the cavy population, we need to look at both sides of the predator-prey system. The grison predation probabilities estimate the probability of an individual cavy being killed or in other words, the percentage of the cavy population taken by the grison; this represents the cavies' perspective. From the grisons' point of view, predation rates are the number of cavies killed per time unit. As animals were not radio-collared randomly, their mortality probabilities do not necessarily equal probabilities of apparent mortality of the entire cavy population, which might be also influenced by other factors, such as population age structure and emigration. Therefore, we did not derive the grison predation rate from the modelled predation probabilities but calculated the observed number of grison kills per telemetry month (= total sum of cavy-telemetry days during the time interval considered/30). We compare the time course of these observed grison predation rates with that of the size of the cavy population as well as the abundance pattern of the main alternative prey, the two water-rat species.

Results

Causes of cavy mortality

Predation was the main proximate cause of mortality for the radio-collared cavies (Table 1). Adult emigration rates were very low, even if all cases of unknown fate are attributed to long-distance dispersal, which seems highly

Table 1. Fate of radio-collared *C. magna* individuals.

Fate	Number (%)
Killed by	
minor grison	58 (56.9)
fox	11 (10.8)
raptors	5 (4.9)
accidental death	1 (1.0)
cause unknown	10 (9.8)
Total dead	85 (85.3)
Fate unknown*	9 (8.8)
Survived**	8 (7.8)
Total radio-collared	102

* 'Fate unknown' includes all cases where we lost the signal and did not catch/recover the animal, (combination of deaths and emigration).

** 'Survived': animals were still alive when the radio-collar were removed, or they were caught again after transmitter failure, but may not have survived until the end of the study period.

unlikely, as some of the transmitters were found later, after the signals had stopped. The grison was the major predator of covies, claiming 78% of the kills in cases where the predator was identified. The other mammalian predator, the fox 'zorro de monte' (*Cerdocyon thous*) was a transient menace, decimating the already small population between June and August 2000, once killing four radio-tagged animals during one day. Whereas when cavy population density was high, raptors (especially the long-winged harrier *Circus buffoni*) were commonly observed circling above the study area, they disappeared almost entirely after the strong decline of the population during summer 2000. Their impact might be slightly underestimated, since cases of unknown fate could represent kills that were carried away outside the transmitters' range.

Mortality probabilities

Overall mortality as well as grison predation probabilities showed a strong temporal variation: models without including a time effect found almost no support (Table 2a, grison predation: $\Delta_i > 30$; Table 2b, overall mortality: $\Delta_i > 14$). For grison predation (Table 2a) the model allowing an interaction between sex and time was selected as by far the best approximating model in the set; the model ranked second achieved considerably less support ($\Delta_i = 6.82$), and was 32 times less likely. This suggests that the probability of grison predation for covies was not only sex-specific but preferences seemed to change over time. Additional sources of mortality (Table 2b, i.e. other predators) tended to equalize sex-specific predation mortality, as based on Akaike weights model S_t was 3.8 times as likely as model $S_{s \times t}$. However, the additive model S_{s+t} was almost equally well supported as the best model ($\Delta S_{s+t} = 1.39$). We repeated

Table 2. Set of candidate models for survival probabilities ($= 1 - \text{mortality}$) of radio-collared *C. magna* for: (a) grison predation and (b) overall mortality. Factors considered are sex (s) and time (t); with time intervals of 3 months. For each model we present: the number of estimable parameters (K), the deviance (DEV), Akaike's information criterion for small samples (AIC_c), the difference between the minimum AIC_c of the top model and the model considered (Δ_i) and Akaike weights (w_i). The best approximating models of the sets (based on AIC_c), are highlighted in bold.

Model	K	DEV	AIC_c	Δ_i	w_i
(a) Grison predation					
$S_{s \times t}$	16	51.29	298.27	0	0.96
S_{s+t}	9	74.80	306.81	8.54	0.01
S_t	8	75.17	305.08	6.82	0.03
S_s	2	112.67	330.24	31.97	0
S	1	113.45	329	30.73	0
(b) Overall mortality					
$S_{s \times t}$	16	68.36	395.29	3.29	0.11
S_{s+t}	9	81.37	393.39	1.39	0.29
S_t	8	82.07	392.00	0	0.59
S_s	2	109.98	407.59	15.59	0
S	1	111.00	406.58	14.59	0

Model notation: S: survival, $s \times t$: interaction term between sex and time, $s+t$: additive effects of sex and time (parallel lines for females and males on a logit-scale); t: time only effect, s: sex effect only, 'no index': constant survival.

the model selection process with the analogous data-sets in which the first two weeks after collaring the animal were left-censored (excluded). Exactly the same model ranking was obtained.

The best approximating model for rates of apparent mortality was $\phi_{s \times t}$, p_{s+t} . As the model ranking second had considerably less support ($\Delta_{\phi_{s \times t}, p_{s+t}} = 2.42$) we based inference only on the best model.

For both sexes the time course of grison predation was very close to the overall mortality of the radio-collared covies (Fig. 1a: females $r_{S(\text{grison})}, S(\text{overall}) = 0.94$, Fig. 1b: males $r_{S(\text{grison})}, S(\text{overall}) = 0.93$). Note that we present the correlation coefficient r only as a measure of the strength of the association between the two curves. The gap between the two curves during winter and spring 2000 was mainly caused by the fox predation as described above. Grison predation and overall mortality probabilities also roughly paralleled those of apparent mortality of the whole cavy population (females: $r_{S(\text{grison})}, \phi = 0.77$, $r_{S(\text{overall})}, \phi = 0.85$; males: $r_{S(\text{grison})}, \phi = 0.88$, $r_{S(\text{overall})}, \phi = 0.93$). During some time intervals, mortality was higher for radio-collared covies than for the whole population, (e.g. around September 1999 for females). However, models in which we left-censored (excluded) the first two weeks after the individuals were fitted with radio collars yielded almost identical estimates (though with much larger standard errors). Most of the time predation probabilities were higher in male than in female covies. It was only during spring 1999 that the risk of grison predation was much higher for females than for males.

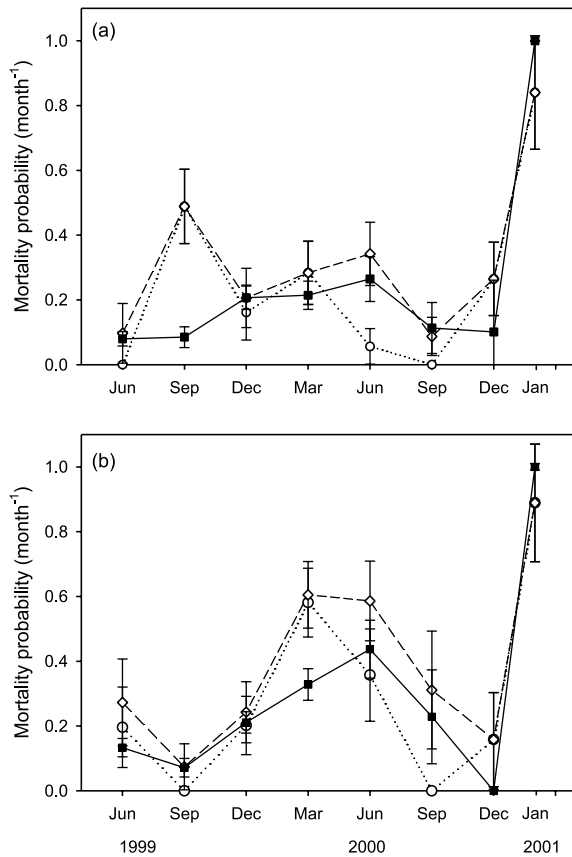


Fig. 1. Monthly probabilities of grison predation (open circles, dotted line), overall mortality (open diamonds, dashed line) and apparent mortality of the entire cavy population (filled squares, solid line) for (a) females and (b) males. Maximum likelihood estimates and standard errors are based on the models $S_{s \times t}$ and $\phi_{s \times t}$, respectively.

Cavy population density and grison predation rates

The cavy population began to decline steeply from late spring 1999 onwards throughout the austral summer months. It stabilised at low numbers during the second winter of the study and, after a slight recovery due to reproduction in spring 2000, it finally went extinct in mid-January 2001 (Fig. 2a). The observed grison predation rate showed a seasonal pattern with the highest predation pressure on the cavy population being during the dry summer months. In both years the increase in grison predation coincided with a strong drop in cavy numbers. Grison predation seemed to depend only partly on cavy density ($r_{\text{grison predation, mean cavy population size}} = -0.29$); when cavy abundance was at its minimum (winter 2000), none of the cavies fitted with radio-collars were killed by grison, nor did we encounter any member of the grison family on the study site during that period. However, despite low cavy numbers at the beginning of the second summer, grison predation increased again and reached its peak when almost all of the remaining

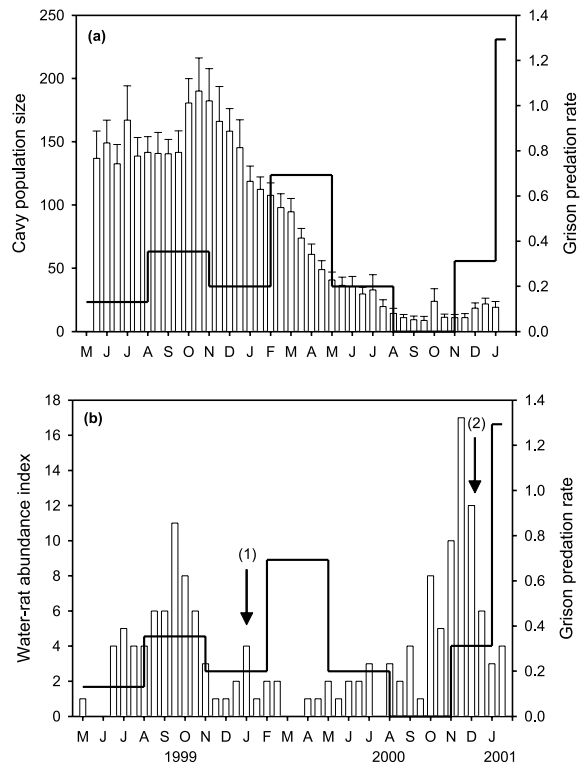


Fig. 2. The 'timing' of events: The observed grison predation rate (grison kills/telemetry-months, thick line) and (a) cavy population size development (bars), (b) water-rat abundance (bars). Evidence for grison reproduction indicated by numbers over bars in (b) where: (1) indicates sightings and captures of members of the grison family (2 adults, 3 sub-adults), and (2) when three pups with eyes still closed were found in the burrow system. Estimates for cavy population size (+1 SE) were derived from probabilities of recapture (Cormack-Jolly-Seber model).

adult cavies (all radio-collared) were taken by grison within one week.

Grison diet and alternative prey

Galictris cuja almost exclusively preyed on small mammals; the only other prey remains found in the faeces were egg shells and parts of the skin of a colubrid snake (*Philodryas*). In late winter, during the period of high cavy density and high water levels (September 1999), the grison distributed its predation pressure more or less evenly amongst both cavy species present (*C. magna* and *C. aperea* remains could not be separated by hair analysis) and two large water-rat species, *Holochilus brasiliensis* and *Scapteromys tumidus* (Table 3). After the area had dried up in summer, we found remains of *Cavia* spp. in every single faecal sample – despite cavy numbers being already very low (only *C. magna* present on the study area in January 2001). The combined abundance of the main alternative prey, the two water-rat species, followed a seasonal pattern with peak

Table 3. Frequency (%F) and number (n) of prey items occurring in the faeces of the minor grison (*Galictis cuja*), collected during September '99 (characterised by high cavy population density and high water level) and January '01 (characterised by low cavy density, low water level).

Prey	September 1999		January 2001	
	n	%F	n	%F
<i>Cavia magna/C. aperea</i>	5	25.0%	47	100%
<i>Holochilus brasiliensis</i>	7	35.0%	2	4.3%
<i>Scapteromys tumidus</i>	5	25.0%	1	2.1%
<i>Akodon azarae</i>	1	5.0%	–	–
Other rodents	2	10.0%	–	–
Snake	–	–	8	17.0%
Eggs (bird)	2	10.0%	–	–
Total	20		47	

numbers in spring due to reproduction, and low numbers during the austral summer months (Fig. 2b). The absolute indices of rat-abundance are not strictly comparable, as the probability of catching rats was probably lower during the first year of the study when high cavy densities resulted in many traps being already filled before the water-rats started with their nocturnal activities.

Grison reproduction

Anecdotal data on grison reproduction suggest that breeding took place in late spring/early summer (Fig. 2b) and that one pair had a litter of three in each year. We repeatedly saw the family or three offspring alone and caught one subadult male, weighing 870 g (~ half of the adult males' body mass) in January 1999. On 15th December 2000 we found three pups with eyes still closed inside a burrow system while digging for a radio-collar.

Discussion

The predictions derived from the hypothesis that predation by the minor grison was the key factor determining the dynamics of the wild cavy population studied were met to a large extent. Predation by the minor grison proved to be the main cause of mortality in our cavy population. Moreover, probabilities of grison predation closely followed that of overall mortality of the radio-tracked fraction of the population most of the time. They also roughly paralleled probabilities of apparent mortality of the entire cavy population, suggesting that grison predation indeed was the single most important factor shaping the mortality patterns of this cavy population. Although the grison ceased to hunt cavies during the lowest population density period, shortly afterwards they specialised on the cavies despite their almost non-existing recovery. This high predation

pressure possibly led to the local extinction of the cavy population.

The impact of radio-collars

The use of radio-tracking enabled us to directly estimate predation probabilities of wild cavies. However, radio-collars may have adverse effects on the behaviour and survival of collared individuals (White and Garrott 1990). As the radio-tracked part of our cavy population, especially females, at times showed lower survival probabilities than the population as a whole, we attempt to assess the impact that radio-collars may have had on the animals.

Firstly, the weight of the radio-packages used was only 0.5–2.0% of the cavy's body mass (compared to 10% for collared lemmings *Dicrostonyx groenlandicus*: Boonstra et al. 1990, root voles *Microtus oeconomus*: Steen 1995, around 5% for snowshoe hares *Lepus timidus*: Keith et al. 1993). Secondly, negative effects of radio-collars on survival are most commonly manifested within the first few days after attachment (Webster and Brooks 1980, Wolton and Trowbridge 1985, Keith 1990, Daly et al. 1992, Reid et al. 1995). However, the repetition of the model selection processes excluding the data obtained during the first two weeks after collar attachment yielded identical results. Finally, it seems unlikely that the sexes differ in their reaction to being collared and that the impact was not consistent over time.

Another possible explanation for differences in the mortality probabilities of collared versus non-collared animals could be that the tracked sub-population was not a random sample of the entire population. We preferentially radio-collared larger, older individuals to reduce risks for not fully grown individuals, especially in the beginning of the study period. Size-specific predation with a preference for large individuals is documented for weasel predation on voles (Norrdahl and Korpimäki 2002). As the average age and body mass declined during the population crash (Kraus, unpubl.), this seems plausible also for our cavy population.

However, even if the mortality probabilities of the radio-collared animals were slightly increased, their similar course with respect to apparent mortality probabilities for the entire population shows that the negative impact was either additive or not strong enough to obscure the effects of the major factor, time. Therefore, we are confident that the estimated predation probabilities reflect the actual mortality patterns of the cavy population.

Proximate causes of cavy mortality

Predation accounted for at least 87% of the deaths of radio-collared cavies, whereas adult emigration played a

negligible role in our study population. We also set traps in neighbouring patches of *Eryngium*, but no marked *C. magna* were caught. Other studies on predator-limited populations report similar percentages (e.g. 80–90% in snowshoe hares, Keith 1990; 82% in collared lemmings, Steen 1995). The minor grison was by far the most important predator of the wild cavy population (78% of the kills). This figure is highly similar to that of a cyclic vole population also preyed upon by small mustelids (77%, Norrdahl and Korpimäki 1995). Like other small mustelids the grison is a highly effective predator as its sleek body allows it to access prey burrows or tunnels through dense vegetation as in the case of cavies. Circumstantial evidence suggests that it hunts cooperatively in small family units (Sunquist et al. 1989 in Diuk-Wasser and Cassini 1998). High prey-capture efficiency has been identified to have a destabilising impact on predator-prey systems (Rosenzweig and MacArthur 1963).

The second important predator, the fox, was only present for a few months at our study site (as we judged by tracks found), but its impact on the cavy population was considerable. This confirms that such stochastic demographic factors can exert a strong effect if population numbers are already low. On the other hand, raptors played only a minor role as cavy predators. Avian predators, including rodent specialists, are thought to have a stabilising effect on small mammal populations due to their nomadic behaviour and ability to concentrate on areas with high prey density (Anderson and Erlinge 1977, Hanski et al. 1991). Dense vegetation probably acts as a significant prey refuge against visually hunting birds of prey. Our observations are consistent with these ideas; whereas at the beginning of the study we frequently found cavy remains left by raptors, diurnal birds of prey almost disappeared after the crash of the cavy population.

The impact of grison predation on cavy population dynamics

Evidence that predators remove a large proportion of the prey population is a necessary, but alone not sufficient condition to prove that predation is the ultimate cause driving population fluctuations (Krebs 1996). The second condition is to show that predation consistently determines mortality patterns over time and does not act simply as a minor additive factor. Mostly, we found that grison predation probabilities were close, at times even identical, to those of overall mortality. It was only during the second winter and spring that other predators (mainly the fox) contributed substantially to the overall mortality probability of the cavy population. During the final decline of the population, grison predation was again the main factor of cavy mortality.

A third necessary condition for the predation hypothesis is that mortality is the dominant demographic process of population change; emigration could exceed mortality or in-situ recruitment and immigration might compensate the population loss. Probabilities of apparent mortality include both mortality and emigration. If these show a different pattern over time compared to mortality alone, it would indicate that emigration played an important role in determining loss rates of the population. In our cavy population, probabilities of overall mortality and apparent mortality were highly similar, and grison predation probabilities also roughly paralleled those of apparent mortality. Population gains obviously did not compensate for the high loss rate due to predation, but they may have slowed down the rate of population decline. A large influx of *C. magna* into our study site in April 1999 resulted in more than 60 unmarked individuals being caught. From then on, immigration only played a negligible role in cavy population dynamics; only 8 previously unmarked adults were caught in 2000. Even in the months of peak reproduction, apparent survival contributed substantially more to the rate of population change λ than recruitment. At other times, population loss rates accounted for around 97% of the rates of population change (Kraus, unpubl.).

Together, the three conditions support the conclusion that grison predation was the dominant factor shaping changes in our study population. Of course, we cannot distinguish if grison predation was really the ultimate or simply the proximate cause behind the observed population dynamics; we do not know if the cavies would have died due to other causes in the near future if no predation had occurred (Krebs 1996). During high cavy densities, signs of overgrazing were evident; the animals' body condition was lower and parasite loads higher than during low density periods (Kraus, unpubl.). However, given the good body condition of animals and the high food availability before the final decline of the population, it seems unlikely that predation acted as a merely compensatory mortality factor. Thus, we conclude that grison predation was the key factor responsible for the population changes observed in our wild cavy population.

Proximate mechanisms – the timing of events

One characteristic of grison predation that did not influence the probabilities of overall mortality was the sex-time interaction supported by the model selection process. The selection of the lesser parameterized model S_t for overall mortality in comparison to the strong support for the more complex one $S_{s \times t}$ for grison predation, cannot be due to small sample size as more individuals are included in the former data-set. Because

the estimated predation probabilities are already corrected for prey availability, and thus for sex ratio, this suggests that the grison showed prey selection. Whereas the grison preferentially took females during the peak of the breeding season, males were mainly targeted during the non-reproductive season. This pattern was not evident during the second reproductive season, but this might be simply because the grison did not appear to hunt at our study site.

Sex-specific predation risk might partly represent a survival cost of reproduction (reviewed by Magnhagen 1991). In polygynous mammals, males are often more susceptible to predation supposedly due to mate-searching activities or male-biased dispersal (Daly et al. 1990, Koivunen et al. 1996). Male *C. magna* used larger home ranges than females and showed less home range fidelity, suggesting higher levels of activity (Kraus et al. 2003). On the other hand, odour, lower agility during pregnancy, and increased conspicuousness due to vocal offspring may all contribute to a heightened predation risk for breeding females (oestrous deer mice *Peromyscus maniculatus bairdi*: Cushing 1985; pregnant *Microtus voles*: Klemola et al. 1997, Norrdahl and Korpimäki 1998). Of the seven cavy females killed by grison during spring 1999, all five that were caught in the trapping session prior to their death were either pregnant or lactating. By the selecting of breeding females, mammalian predation has an especially high potential to stunt their prey's population growth (Klemola et al. 1997, Norrdahl and Korpimäki 1998).

Grison predation rates were not directly dependent on cavy densities, in agreement with a rather destabilising effect on the population dynamics. A seasonal pattern seemed to be a characteristic feature of grison predation; predation rates showed a pronounced peak during the dry summer months. As the greatest population growth of cavies occurred during the austral spring months, the time-delay of the onset of maximum predation pressure may have further added to the detrimental effect of grison predation on cavy numbers.

Generalist predators are normally thought to stabilise their prey's dynamics through a functional response type III (S-shaped curve), mediated by switching to alternative species when main prey numbers drop (Anderson and Erlinge 1977, Erlinge 1984, Hanski et al. 1991, Turchin and Ostfeld 1997). At our study site, the main alternative prey were two large water-rat species (*Scapteromys tumidus* and *Holochilus brasiliensis*), confirming that grisons hunt relatively large prey (Ebensperger et al. 1991). So why did the grison, a known generalist predator (Ebensperger et al. 1991, Diuk-Wasser and Cassini 1998), not switch to these alternative prey species when cavies became rare? As both rat species (especially *Holochilus brasiliensis*) are adapted to wet habitats, many individuals are thought to 'migrate' towards the nearby lagoon when the study area dries up during the

summer (Gambarotta, pers. comm.). This lack of alternative prey may have forced the grison to concentrate on cavies during summer and thus, to switch its functional role from a generalist to a specialist predator, resulting in a strong, destabilising impact on the cavies' population dynamics.

However, grison predation rates were not strictly coupled to rat-numbers either; predation pressure on cavies had already declined in autumn, before rat numbers had substantially increased. We suspect that the timing of grison reproduction aggravated the cavies' situation during summer as litters were produced in late spring. This increased the predator-prey ratio resulting in intensified predation pressure on the cavies (a small-scale 'numerical response'). Thus, the decline in alternative prey in summer coincided with high grison food demands (due to reproduction). We speculate that this interaction caused the extremely high predation pressure on cavies at this time of the year, which finally led to the local extinction of the study population.

Although only few studies have been conducted on caviomorph populations, several cases of local extinction are documented (desert cavies *Microcavia australis* by the minor grison, Rood 1970, 1972; plains viscacha *Lagostomus maximus* by the mountain lion *Felis concolor*, Branch et al. 1994). During this study, apart from the described *C. magna* population, the co-inhabiting population of *C. aperea* vanished even faster. In Argentina, a population of yellow-toothed cavies *Galea musteloides* went extinct and another one declined rapidly until a grison was removed from the study site (Asher, pers. comm.).

The life history of caviomorphs is rather atypical for small mammals; after long gestation periods (> two months in the case of *C. magna*) they produce litters of few but highly precocial offspring (*C. magna*: 1–2, Kraus, unpubl.). Therefore, the natural rate of increase is low in comparison to other small mammals such as voles which have realised rates of increase about 7, but up to 16 yr⁻¹ (Turchin and Ostfeld 1997, Klemola et al. 2002). This not only causes an intrinsic delay in the response to favourable extrinsic events, such as increased plant productivity (Branch et al. 1994, Meserve et al. 1995), but also makes it difficult to compensate for losses, such as heavy predation or stochastic demographic events. We believe that due to these low reproductive rates, wild cavy populations are likely to be particularly susceptible to local extinction, independent of the dominant factors responsible for strong population declines.

Conclusion

Our study of a little known predator-prey system provides another example of the high potential small

mustelid predators have to limit their prey populations (Norrdaahl and Korpimäki 1995, 1998, Barreto and MacDonald 2000, Telfer et al. 2001). The proximate mechanisms were similar to those described for predator-prey systems in northern latitudes: the lack of alternative prey coincided with the grison reproductive season causing the grison to specialise on cavies. The onset of this high predation pressure occurred with a time-delay with respect to the cavies' peak reproduction. The fact that the grison preferentially preyed upon breeding females may have further contributed to the strongly destabilising impact that the interaction of these factors had on cavy population numbers. The precocial wild cavies with their low reproductive output, may be particularly susceptible to local extinction. On the other hand, with their highly mobile offspring they are good colonisers and local migrations between suitable habitat patches are documented (Galante and Cassini 1994, Bilenca et al. 1995, Kraus et al. 2003). These features could prove interesting for future metapopulation studies.

Acknowledgements – This study was conducted in cooperation between the Facultad de Ciencias of the Universidad de la Republica in Montevideo, Uruguay through Mario Clara and the Department of Animal Behaviour, University of Bielefeld. Permission for fieldwork was granted by the Ministerio de Ganadería, Agricultura y Pesca (MGAP). Fritz Trillmich and Joachim Künkele helped enthusiastically in the field and substantially improved this manuscript. Juan Carlos Gambarotta and Gabriela Rodríguez Gambarotta provided invaluable support with logistic, bureaucratic as well as everyday problems. Alvaro Saralegui and Ramiro Pereira excellently led the project during our absence. Special thanks go to Inés de Rosa, Lorena Erbure, Fabián Benítez, Andrés de Mello and Carlos Calimares for their help with fieldwork. Thanks also go to David Thomson for introducing CK to program MARK, and to Florian Lengyel for improving our English. The study was financially supported by the Deutsche Forschungsgemeinschaft (DFG) and the Graduiertenförderung of Nordrhein Westfalen.

References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. – In: Petrov, B. N. and Csaki, F. (eds), Second Int. Symp. on Information Theory. Akademiai Kiado, pp. 267–281.

Akaike, H. 1985. Prediction and entropy. – In: Atkinson, A. C. and Fienberg, S. E. (eds), A celebration of statistics. Springer-Verlag, pp. 1–24.

Akçakaya, H. R. 1992. Population cycles of mammals: evidence for a ratio-dependent predation hypothesis. – *Ecol. Monogr.* 62: 119–142.

Anderson, D. R. and Erlinge, S. 1977. Influence of predation on rodent populations. – *Oikos* 29: 591–597.

Angelstam, P., Lindström, E. and Widén, P. 1984. Role of predation in short-term fluctuations of some birds and mammals in Fennoscandia. – *Oecologia* 62: 199–208.

Asher, M. and Sachser, N. 2000. Habitat selection and social system in a population of wild guinea pigs (*Cavia aperea*) under natural conditions. – *Zoology* 103: 25.

Barreto, G. R. and MacDonald, D. W. 2000. The decline and local extinction of a population of water voles, *Arvicola*

terrestris, in southern England. – *Z. Säugetierkd.* 65: 110–120.

Bilenca, D. N., Cittadino, E. A. and Kravetz, F. O. 1995. Influencia de la actividad de *Cavia aperea* sobre la estructura del habitat y la distribución de *Akodon azarae* y *Oryzomys flavescens* (Rodentia: Caviidae, Muridae) en bordes de cultivos de la región pampeana (Argentina). – *Iheringia. Sér. Zool., Porto Alegre* 79: 67–75.

Boonstra, R. 1977. Predation on *Microtus townsendii* populations: impact and vulnerability. – *Can. J. Zool.* 55: 1631–1643.

Boonstra, R., Krebs, C. J. and Kanter, M. 1990. Arctic ground squirrel predation on collared lemmings. – *Can. J. Zool.* 68: 757–760.

Branch, L. C., Villarreal, D. and Fowler, G. S. 1994. Factors influencing population dynamics of the plains vizcacha (*Lagostomus maximus*, Mammalia, Chinchillidae) in scrub habitat of central Argentina. – *J. Zool., Lond.* 232: 383–395.

Burnham, K. P. and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretic approach. – Springer-Verlag.

Cassini, M. H. 1991. Foraging under predation risk in the wild guinea pig. – *Oikos* 62: 20–24.

Corbett, L. K. and Newsome, A. E. 1987. The feeding ecology of the dingo. III. Dietary relationships with widely fluctuating prey populations in arid Australia: an hypothesis of alternation of predation. – *Oecologia* 74: 215–227.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. – *Biometrika* 51: 429–438.

Côté, I. M. and Sutherland, W. J. 1997. The effectiveness of removing predators to protect bird populations. – *Conserv. Biol.* 11: 395–405.

Cushing, B. S. 1985. Estrous mice and vulnerability to weasel predation. – *Ecology* 66: 1976–1978.

Daly, M., Wilson, M. I., Behrends, P. R. et al. 1990. Characteristics of kangaroo rats, *Dipodomys merriami*, associated with differential predation risk. – *Anim. Behav.* 40: 380–389.

Daly, M., Wilson, M. I., Behrends, P. R. et al. 1992. Sexually differentiated effects of radio transmitters on predation risk and behaviour in kangaroo rats *Dipodomys merriami*. – *Can. J. Zool.* 70: 1851–1855.

Diuk-Wasser, M. A. and Cassini, M. H. 1998. A study on the diet of the minor grison and a preliminary analysis of their role in the control of rabbits in Patagonia. – *Stud. Neotrop. Fauna Environm.* 33: 3–6.

Ebensperger, L. A., Mella, J. E. and Simonetti, J. A. 1991. Trophic-niche relationships among *Galictis cuja*, *Dusicyon culpaeus*, and *Tyto alba* in central Chile. – *J. Mammal.* 72: 820–823.

Erlinge, S., Göransson, G., Hansson, L. et al. 1983. Predation as a regulating factor on small rodent populations in southern Sweden. – *Oikos* 40: 36–52.

Erlinge, S., Göransson, G., Högstedt, G. et al. 1984. Can vertebrate predators regulate their prey? – *Am. Nat.* 123: 125–133.

Erlinge, S., Göransson, G., Högstedt, G. et al. 1988. More thoughts on vertebrate predator regulation of prey. – *Am. Nat.* 132: 148–154.

Errington, P. L. 1946. Predation and vertebrate populations. – *Q. Rev. Biol.* 21: 144–177–221–245.

Errington, P. L. 1956. Factors limiting higher vertebrate populations. – *Science* 124: 304–307.

Fitzgerald, B. M. 1977. Weasel predation on cyclic populations of the montane vole (*Microtus montanus*) in California. – *J. Anim. Ecol.* 46: 367–397.

Galante, M. L. and Cassini, M. H. 1994. Seasonal variation of a cavy population in the Pampa region, east-central Argentina. – *Mammalia* 58: 549–556.

Gambarotta, J. C., Saralegui, A. M. and Gonzáles, E. 1999. Vertebrados tetrápodos del Refugio de Fauna Laguna de

- Castillos, Depto de Rocha. – Relevamientos de Biodiversidad 3: 1–31.
- Graham, L. H. and Lambin, X. 2002. The impact of weasel predation on cyclic field-vole survival: the specialist predator hypothesis contradicted. – *J. Anim. Ecol.* 71: 946–956.
- Hanski, I. 1987. Populations of small mammals cycle – unless they don't. – *Trends Ecol. Evol.* 2: 55–56.
- Hanski, I., Hansson, L. and Henttonen, H. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. – *J. Anim. Ecol.* 60: 353–367.
- Hanski, I., Henttonen, H., Korpimäki, E. et al. 2001. Small-rodent dynamics and predation. – *Ecology* 82: 1505–1520.
- Hanski, I., Turchin, P., Korpimäki, E. et al. 1993. Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. – *Nature* 364: 232–235.
- Hansson, L. 1984. Predation as the factor causing extended low densities in microtine cycles. – *Oikos* 43: 255–256.
- Hansson, L. and Henttonen, H. 1988. Rodent dynamics as community processes. – *Trends Ecol. Evol.* 3: 195–200.
- Henttonen, H., Oksanen, T., Jortikka, A. et al. 1987. How much do weasels shape microtine cycles in the northern Fennoscandian taiga? – *Oikos* 50: 353–365.
- Jaksić, F. M. 1986. Predation upon small mammals in shrublands and grasslands of southern South America: ecological correlates and presumable consequences. – *Rev. Chil. Hist. Nat.* 59: 209–221.
- Jaksić, F. M., Jiménez, J. E., Castro, S. A. et al. 1992. Numerical and functional response of predators to a long-term decline in mammalian prey at a semi-arid Neotropical site. – *Oecologia* 89: 90–101.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. – *Biometrika* 52: 225–247.
- Jonsson, P., Koselka, E. and Mappes, T. 2000. Does risk of predation by mammalian predators affect the spacing behaviour of rodents? Two large scale experiments. – *Oecologia* 122: 487–492.
- Karels, T. J., Byrom, A. E., Boonstra, R. et al. 2000. The interactive effects of food and predators on reproduction and overwinter survival of arctic ground squirrels. – *J. Anim. Ecol.* 69: 235–247.
- Keith, L. B. 1990. Dynamic of snowshoe hare population. – *Curr. Mammal.* Vol. 2.
- Keith, L. B., Bloomer, S. E. M. and Willebrand, T. 1993. Dynamics of a snowshoe hare population in fragmented habitat. – *Can. J. Zool.* 71: 1385–1392.
- Klemola, T., Koivula, M., Korpimäki, E. et al. 1997. Small mustelid predation slows population growth of *Microtus* voles: a predator reduction experiment. – *J. Anim. Ecol.* 66: 607–614.
- Klemola, T., Koivula, M., Korpimäki, E. et al. 2000. Experimental tests of predation and food hypotheses for population cycles of voles. – *Proc. R. Soc. Lond. B* 267: 351–356.
- Klemola, T., Korpimäki, E. and Koivula, M. 2002. Rate of population change in voles from different phases of the population cycle. – *Oikos* 96: 291–298.
- Koivunen, V. E., Korpimäki, E. and Hakkarainen, H. 1996. Differential avian predation on sex and size classes of small mammals: doomed surplus or dominant individuals? – *Ann. Zool. Fenn.* 33: 293–301.
- Korpimäki, E. and Krebs, C. J. 1996. Predation and population cycles of small mammals. A reassessment of the predation hypothesis. – *BioScience* 46: 754–764.
- Korpimäki, E. and Norrdahl, K. 1998. Experimental reduction of predators reverses the crash phase of small-rodent cycles. – *Ecology* 79: 2448–2455.
- Korpimäki, E., Norrdahl, K. and Rinta-Jaskari, T. 1991. Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? – *Oecologia* 88: 552–561.
- Korpimäki, E., Norrdahl, K. and Valkama, J. 1994. Reproductive investment under fluctuating predation risk: microtine rodents and small mustelids. – *Evol. Ecol.* 8: 357–368.
- Korpimäki, E., Norrdahl, K., Klemola, T. et al. 2002. Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. – *Proc. R. Soc. Lond. B* 269: 991–997.
- Kraus, C., Künkele, J. and Trillmich, F. 2003. Spacing behaviour and its implications for the mating system of a precocial small mammal: an almost asocial cavy (*Cavia magna*)? – *Anim. Behav.* 66: 225–238.
- Krebs, C. J. 1996. Population cycles revisited. – *J. Mammal.* 77: 8–24.
- Krebs, C. J., Boutin, S., Boonstra, R. et al. 1995. Impact of food and predation on the snowshoe hare cycle. – *Science* 269: 1112–1115.
- Krebs, C. J., Boutin, S., Boonstra, R. et al. 2000. Cyclic dynamics in field vole populations and generalist predation. – *J. Anim. Ecol.* 69: 106–118.
- Krebs, C. J., Boonstra, R., Boutin, S. et al. 2001. What drives the 10-year cycle of snowshoe hares? – *BioScience* 51: 25–35.
- Lambian, X., Petty, S. J. and MacKinnon, J. L. 2000. Cyclic dynamics in field vole populations and generalist predation. – *J. Anim. Ecol.* 69: 106–118.
- Lebreton, J.-D., Burnham, K. P., Clobert, J. et al. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – *Ecol. Monogr.* 62: 67–118.
- Lee, E. T. 1992. Statistical methods for survival data analysis. – John Wiley and Sons.
- Lidicker, W. Z. J. 2000. A food/landscape interaction model for microtine rodent density cycles. – *Oikos* 91: 435–445.
- Magnhagen, C. 1991. Predation risk as a cost of reproduction. – *Trends Ecol. Evol.* 6: 183–186.
- May, R. M. 1981. Models for single populations. – In: May, R. M. (ed.), *Theoretical ecology: principles and applications*. Blackwell, pp. 5–29.
- Meserve, P. L., Gutiérrez, J. R. and Jaksić, F. M. 1993. Effects of vertebrate predation on a caviomorph rodent, the degu (*Octodon degus*) in a semiarid thorn scrub community in Chile. – *Oecologia* 94: 153–158.
- Meserve, P. L., Yunker, J. A., Gutiérrez, J. R. et al. 1995. Heterogeneous responses of small mammals to an El Niño Southern Oscillation event in northcentral semiarid Chile and the importance of ecological scale. – *J. Mammal.* 76: 580–595.
- Meserve, P. L., Gutiérrez, J. R., Yunker, J. A. et al. 1996. Role of biotic interactions in a small mammals assemblage in semiarid Chile. – *Ecology* 77: 133–148.
- Norrdahl, K. and Korpimäki, E. 1993. Predation and interspecific competition in two *Microtus* voles. – *Oikos* 66: 149–158.
- Norrdahl, K. and Korpimäki, E. 1995. Mortality factors in a cyclic vole population. – *Proc. R. Soc. Lond. B* 261: 53.
- Norrdahl, K. and Korpimäki, E. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators. – *Ecology* 79: 226–232.
- Norrdahl, K. and Korpimäki, E. 2002. Changes in individual quality during a 3-year population cycle of voles. – *Oecologia* 130: 239–249.
- Pearson, O. P. 1964. Carnivore-mouse predation: an example of its intensity and bioenergetics. – *J. Mammal.* 45: 177–188.
- Pearson, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. – *J. Anim. Ecol.* 35: 217–233.
- Pearson, O. P. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). – *J. Mammal.* 52: 41–49.
- Pech, R. P., Sinclair, A. R. E., Newsome, A. E. et al. 1992. Limits to predator regulation of rabbits in Australia: evidence from predator-removal experiments. – *Oecologia* 89: 102–112.
- Reid, D. G., Krebs, C. J. and Kenney, A. 1995. Limitation of collared lemming population growth at low densities by predation mortality. – *Oikos* 73: 387–398.

- Rood, J. P. 1970. Ecology and social behavior of the desert cavy (*Microcavia australis*). – *Am. Midl. Nat.* 83: 415–454.
- Rood, J. P. 1972. Ecological and behavioural comparisons of three genera of argentine caviés. – *Anim. Behav. Monogr.* 5: 1–83.
- Rosenzweig, M. L. and MacArthur, R. H. 1963. Graphical representation and stability conditions of predator–prey interactions. – *Am. Nat.* 97: 209–223.
- Royama 1992. Analytical population dynamics. – Chapman and Hall.
- Seber, G. A. F. 1965. A note on the multiple-recapture census. – *Biometrika* 52: 249–259.
- Sinclair, A. R. E. 1989. Population regulation in animals. – In: Cherrett, J. M. (ed.), *Ecological concepts*. Blackwell, pp. 197–241.
- Sinclair, A. R. E. and Pech, R. P. 1996. Density dependence, stochasticity, compensation and predator regulation. – *Oikos* 75: 164–173.
- Sinclair, A. R. E., Olsen, P. D. and Redhead, T. D. 1990. Can predators regulate small mammal populations? Evidence from house mouse outbreaks in Australia. – *Oikos* 59: 382–392.
- Skogland, T. 1991. What are the effects of predators on large ungulate populations? – *Oikos* 61: 401–411.
- Sommer, S. 2000. Sex-specific predation on a monogamous rat, *Hypogeomys antimena* (Muridae: Nesomyinae). – *Anim. Behav.* 59: 1987–1994.
- Steen, H. 1995. Untangling the causes of disappearance from a local population of root voles, *Microtus oeconomus*: a test of the regional synchrony hypothesis. – *Oikos* 73: 65–72.
- Stenseth, N. C., Bjornstad, O. N. and Falck, W. 1996. Is spacing behaviour coupled with predation causing the microtine density cycle? A synthesis of current process-oriented and pattern-oriented studies. – *Proc. R. Soc. Lond. B* 263: 1423–1435.
- Tanner, J. T. 1975. The stability and the intrinsic growth rates of prey and predator populations. – *Ecology* 56: 855–867.
- Teerink, B. J. 1991. Hair of west European mammals. Atlas and identification key. – Cambridge Univ. Press.
- Telfer, S., Holt, A., Donaldson, R. and Lambin, X. 2001. Metapopulation processes and persistence in remnant water vole populations. – *Oikos* 95: 31–42.
- Trout, R. C. and Titensor, A. M. 1989. Can predators regulate wild rabbit *Oryctolagus cuniculus* population density in England and Wales? – *Mammal Rev.* 19: 153–173.
- Turchin, P. and Ostfeld, R. S. 1997. Effects of density and season on the population rate of change in the meadow vole. – *Oikos* 78: 355–361.
- Webster, A. B. and Brooks, R. J. 1980. Effects of radio-transmitters on the meadow vole, *Microtus pennsylvanicus*. – *Can. J. Zool.* 58: 997–1001.
- White, G. C. and Garrott, R. A. 1990. Analysis of wildlife radio-tracking data. – Academic Press.
- White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – *Bird Study* 46: 120–139.
- Wolton, R. J. and Trowbridge, B. J. 1985. The effects of radio-collars on wood mice, *Apodemus sylvaticus*. – *J. Zool., Lond.* 206: 225–239.
- Ylönen, H., Jacob, J., Davies, M. J. et al. 2002. Predation risk and habitat selection of Australian house mice *Mus domesticus* during an incipient plague: desperate behaviour due to food depletion. – *Oikos* 99: 284–289.