Research paper

What is the appropriate timescale for measuring costs of reproduction in a 'capital breeder' such as the aspic viper?

X. BONNET[1,2]*, G. NAULLEAU[1], R. SHINE[2] and O. LOURDAIS[1]
[1]*Conseil Général Des Deux Sèvres, CEBC, CNRS, Villiers en Bois, France;* [2]*Biological Sciences A08, University of Sydney, Australia*
*(*author for correspondence, fax: 33 49 09 65 26; e-mail: bonnet@cebc.cnrs.fr)*

Abstract. Before we can quantify the degree to which reproductive activities constitute a cost (i.e., depress an organism's probable future reproductive output), we need to determine the timescale over which such costs are paid. This is straightforward for species that acquire and expend resources simultaneously (income breeders), but more problematical for organisms that gather resources over a long period and then expend them in a brief reproductive phase (capital breeders). Most snakes are capital breeders; for example, female aspic vipers (*Vipera aspis*) in central western France exhibit a 2- to 3-year reproductive cycle, with females amassing energy reserves for one or more years prior to the year in which they become pregnant. We use long-term mark-recapture data on free-living vipers to quantify the appropriate timescale for studies of reproductive costs. Annual survival rates of female vipers varied significantly during their cycle, such that estimates of survival costs based only on years when the females were 'reproductive' (i.e., produced offspring) substantially underestimated the true costs of reproduction. High mortality in the year after reproducing was apparently linked to reproductive output; low energy reserves (poor body condition) after parturition were associated with low survival rates in the following year. Thus, measures of cost need to consider the timescale over which resources are gathered as well as that over which they are expended in reproductive activities. Also, the timescale of measurement needs to continue long enough into the post-reproductive period to detect delayed effects of reproductive 'decisions'.

Key words: body condition, capital breeder, energy stores, foraging, snake, *Vipera aspis*

Introduction

One of the primary aims of life-history theory is to facilitate comparisons among different kinds of organisms. Only in this way, by examining diverse taxa in a single conceptual framework, can we hope to derive general insights. One of the great successes in this respect has been the development of theory concerning costs of reproduction and the allied concept of Reproductive Effort. The field is based upon an original idea by Williams (1966a, b): the realisation that an iteroparous organism will maximise its lifetime reproductive success not by maximising effort at the first reproductive opportunity, but by

reproducing at a level that does not too greatly reduce its probable future output. This notion has been incorporated into elegant mathematical models (e.g., Schaffer, 1974; Winkler and Wallin, 1987; Sibly and Calow, 1984; Jönsson et al., 1995a, b), and has stimulated extensive empirical studies on a diverse array of species (e.g., Bell, 1980; Bell and Koufopanou, 1986; Clutton-Brock, 1991).

In the present paper, we point out an important complication in measuring the costs of reproduction: we have to be careful about specifying what activities are included under our definition of reproduction. The significance of this superficially trivial caveat is that organisms differ in the timescale over which various components of 'reproductive' activities are carried out. In particular, some animals concentrate all of the activities associated with reproduction (i.e., acquisition as well as expenditure of energy) in a single time period. For these income breeders (Drent and Daan, 1980; Jönsson, 1997), we can evaluate costs of reproduction by comparing energy balance and survival rates between reproductive and non-reproductive animals (e.g., Bell and Koufopanou, 1986) or by documenting the effects of manipulating reproductive expenditure (e.g., Tombre and Erikstad, 1996; Cichon et al., 1998). The situation is more complex with capital breeders that rely upon stored energy reserves to support reproductive output. For such taxa, energy acquisition and expenditure are temporally dissociated, so that measurements of cost taken during the period of reproductive expenditure will fail to include the components of cost that accrue during the energy-gathering phase.

Timescales of reproductive costs

Much of the scientific literature on costs of reproduction is based on studies of birds, and one technique that is often used is to manipulate reproductive expenditure by adding or removing eggs from the nest at the beginning of the period of parental care (e.g., Nur, 1988; Tombre and Erikstad, 1996; Cichon et al., 1998). Importantly, the facet of reproductive effort that is being affected by this manipulation is the level of the parents' foraging effort to provide the nestling. If we compare this situation to that of a viviparous snake such as our study organism, the aspic viper, the contrast becomes obvious. Female aspic vipers produce litters only once every two or three years (or less often), with the intervening ('non-reproductive') years being used to amass energy reserves that will fuel the eventual litter (Naulleau et Bonnet, 1996). Females may eat relatively little during gestation; indeed, some may become completely anorexic (Saint Girons, 1952, 1957a, b). For such an animal, most of the foraging effort occurs over a period of years prior to the year of reproductive output. If we evaluate costs of reproduction in such an organism by comparing females in

'reproductive' versus 'non-reproductive' years of their cycles, then we completely fail to assess the kind of reproductive cost (risk, etc., due to additional foraging) that has been the primary focus of studies on income-breeding species such as most birds. Any comparison of such costs between a bird and a snake – exactly the kind of comparison that is an aim of life-history theory – would be invalidated if we measured different components of cost in the two taxa.

One interesting aspect of the bird–snake comparison is that the validity of such a comparison will depend on the currency in which costs are to be measured. If the currency is energetics, then it may be meaningful to measure total energy allocation to the reproductive event in both taxa, and to measure this trait over the period of expenditure only. Despite the fact that the bird may have gathered the energy over a period of weeks and the snake over a period of years, their allocation of energy to reproduction is still directly comparable. Thus, for example, one could compare total reproductive allocation to body size between these two taxa. Unfortunately, the comparison breaks down as soon as we try to compare energy allocation to reproduction *vs.* to other activities (maintenance, growth, etc.). At this point, the timescale becomes important – and for the reptile, the appropriate timescale is surely that over which these resources have been gathered, not just the 'reproductive' year. The problem is even worse for survival rates, the other main potential currency in which costs can be assessed (and probably, the most important such currency for many kinds of animals – Shine and Schwarzkopf, 1992). By analogy with the bird, the real survival cost of reproduction for a female viper involves the risks that she takes throughout the 'non-reproductive' (energy acquisition) years as well as her risk during reproduction itself.

Unfortunately for the logistics of assessing costs of reproduction, the vast majority of living species probably depend to a significant degree on stored reserves to fuel reproductive expenditure. This characteristic is particularly common in ectothermic species, for several reasons (Pough, 1980; Bonnet *et al.*, 1998). Ectotherms may also differ from endotherms in the timescale over which costs are expressed after the overt reproductive expenditure. Because endotherms (especially birds) are under strong energetic constraints, even a brief period of unfavourable energy balance may be fatal (e.g., Pough, 1980). In contrast, the low metabolic requirements of ectotherms mean that any effect of reproductive expenditure on survival may not be apparent for a much longer period. For example, a bird that compromises its energy reserves or thermoregulatory efficiency due to reproductive costs may thereby die the following winter (e.g., McCleery *et al.*, 1996; Daan *et al.*, 1996; Nilsson and Svensson, 1996) whereas a reptile in the same situation can simply hibernate (which requires very little energy expenditure: Gregory, 1982) over the entire winter period, and not have to face the consequences of its reduced energy reserves

until the following spring. We stress, however that there is a continuum of timescales, and that some birds will resemble some reptiles in important respects. The difference is one of degree, but nonetheless may often be so substantial that we need studies on 'costs' experienced by both kind of organisms. Even superficially similar phenomena in different types of organisms may differ in important respects. For example, high mortality in some passerines and small mammals in the year following breeding (i.e. Gustafsson and Sutherland, 1988) is not directly comparable to the delayed post-reproductive decrease of survival in snakes. The 'delayed survival costs' paid by small endotherms occur after several reproductive episodes (3–5 clutches [litters] per year on average); but after a single reproductive episode in the snakes.

Previous research on costs of reproduction in reptiles has concentrated primarily on events during the actual period of reproductive expenditure: for example, the decrease in survival rates, food intake and mobility of gravid females (e.g., Shine, 1980; Seigel et al., 1987; Madsen and Shine, 1993). Our 6-year mark-recapture study of free-ranging vipers allows us to document these costs over a longer timespan (i.e., the female's entire reproductive cycle, not simply the year in which she produces offspring). We examined the data to calculate the proportion of the total survival costs of reproduction that accrue during different phases of the female cycle. If the probability of survival is very high during 'non-reproductive' years, and very low during 'reproductive' years, then estimates based only on the latter timeframe may nonetheless provide a reasonable index of overall survival costs. However, if survival rates are low during other phases of the cycle, then measurements restricted to 'reproductive' years may substantially underestimate the true costs of reproduction (Jönsson et al., 1995a, b).

If we can quantify survival rates at each stage of the female's cycle, we can compare the magnitude of pre-breeding, breeding and post-breeding components of the overall cost of reproduction. This comparison would be impossible in an income breeder, because the costs of energy acquisition and offspring production occur simultaneously, whereas they are separated temporally in a capital breeder. The relative magnitude of post-breeding costs is also likely to differ in consistent ways between ectotherms and endotherms, because the high metabolic rates of the latter group mean that over-depletion of energy reserves during reproduction is likely to cause death rapidly. Such an effect may well be postponed for a very long period in an organism with lower metabolic needs, such as a viperid snake. To evaluate whether or not reproducing vipers pay long-term costs in survival, we can use the comparison among years of a female's cycle (above). A higher rate of mortality in the year immediately after parturition would support the notion of 'delayed' survival costs. Also, we can compare survival rates in that post-partum year to a female's body condition immediately after she has reproduced in the preceding year.

Materials and methods

Aspic vipers (*Vipera aspis*) are medium-sized (average adult = 48.5 cm snout-vent length, 85.5 g) venomous snakes widely distributed through Europe. We studied a population in central western France (Les Moutiers en Retz), in a mosaic of meadowland and thicker vegetation. The snakes were hand-captured and individually-marked (scale clipping or, later in the study [1993] with electronic tags, sterile transponder TX 1400L, Rhône Mérieux, Destron/IDI INC). Recapture rates were high and emigration was extremely rare, because the snakes are very sedentary (Naulleau *et al.*, 1996) and the 33-ha study area is bounded by habitat unsuitable for this species. Thus, snakes that disappeared had almost certainly died rather than emigrated. To ensure that the lower catchability of non-reproductive females relative to reproductive females did not falsify our results, we waited at least 2 years to classify a given female as dead or not (and thus we did not score survival of females caught in 1996 or 1997). Further details on the study area and our methods are given elsewhere (Bonnet and Naulleau, 1996; Naulleau and Bonnet, 1996; Naulleau *et al.*, 1996; Bonnet *et al.*, 2000). Female vipers in this population typically reproduce within a 2–3-year cycle, although many females do not live long enough to produce more than a single litter (Naulleau *et al.*, in prep.). Litters consist of 1–13 large (17.9 ± 1.2 cm SVL, 6.3 ± 1.1 g) neonates. Females with a body size greater than the minimal size at which parturition has been recorded (41.5 cm SVL, 47 cm total length) were considered as adult.

For the analysis of survival rates in each year of the reproductive cycle, we had to classify females with respect to their stage of the cycle. This procedure was straightforward for reproductive females, and for non-reproductive females 1–4 years after reproduction (post-reproductive), but more problematical for females that were pre-reproductive – i.e., those that were in the years prior to their first 'intended' litter. The individuals allocated to this category were those that we caught one to four years before they first reproduced. In order to qualify as pre-reproductive, the animals had to be in relatively good body condition at the first capture (indicating that they were not post-parturient: e.g. absence of flaccid abdomen or extensive skin folds), and they needed to have been regularly recaptured (so that we were sure that they did not produce a litter during this period). Some of them were first caught as juveniles (based on their small size) and later recaptured after they had attained adult body size but before their first reproduction. In practice, the maternal body-condition threshold for breeding in this species is so consistent (Naulleau and Bonnet, 1996) that it was possible to classify such females with confidence. Females increase steadily in condition throughout the 'non-reproductive' years of their cycle (Fig. 1). Each female was represented only once in the analyses. In total, data on 527 adult females was used in the following analyses.
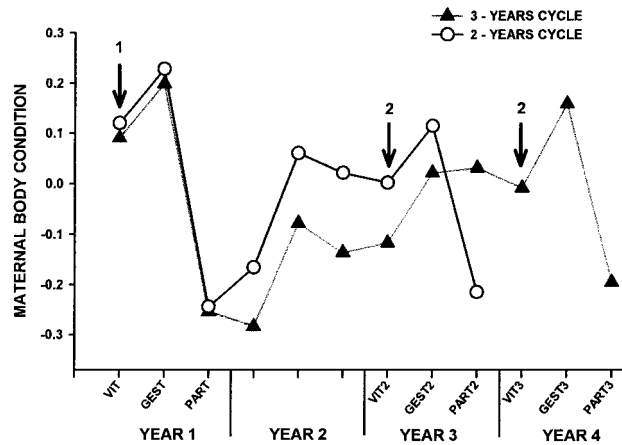
Figure 1. Patterns of change in maternal body condition (residual score from the general linear regression of ln-transformed mass versus snout-vent length) over the course of the reproductive cycle in female vipers, *Vipera aspis*. Females lose considerable body condition at parturition (because of the mass of the litter) and must gradually recover this condition over a period of 2–4 years before they can reproduce again. The figure provides data from females reproducing on a 2-year (circles and black lines) or 3-year (triangles and grey lines) cycle length. 'Vit' = During the period of vitellogenesis; 'gest' = during gestation; 'part' = after parturition. Arrows indicate the onset of vitellogenesis in a given year (1 = first reproduction, 2 = second reproduction).

Results

Figure 2 shows that survival rates varied significantly over the course of the female's reproductive cycle ($\chi^2 = 35.2$, $df = 3$, $p < 0.0001$, all sample sizes indicated in Fig. 2). Female vipers experienced very high mortality (46%) in years when they 'reproduced' (i.e., initiated vitellogenesis and [if they survived] produced offspring). This rate of mortality was significantly higher than that exhibited by females at other stages of their reproductive cycles (*vs*. pre-reproductive females: $\chi^2 = 30.7$, $df = 1$, $p < 0.0001$; *vs*. females 1 year after parturition: $\chi^2 = 4.2$, $df = 1$, $p = 0.041$; *vs*. females 2 years after reproduction: $\chi^2 = 6.9$ [Yates correction], $df = 1$, $p = 0.01$). Mortality rates were also high in the year following parturition (32.5% of snakes died), but were relatively low in other years of the cycle (e.g., annual mortality rate was only 16% 2 years after parturition). Survival was particularly high (80%) for females in the year immediately preceding reproduction, when they were in very good body condition (Figure 2).

We can use these data to estimate the relative magnitude of each component of cost. The total survival cost of reproduction for a female aspic viper can be divided into three components:

(1) *Pre-breeding cost*. This is the decrease in survival probability caused by the female delaying reproduction past the time when she has attained adult body
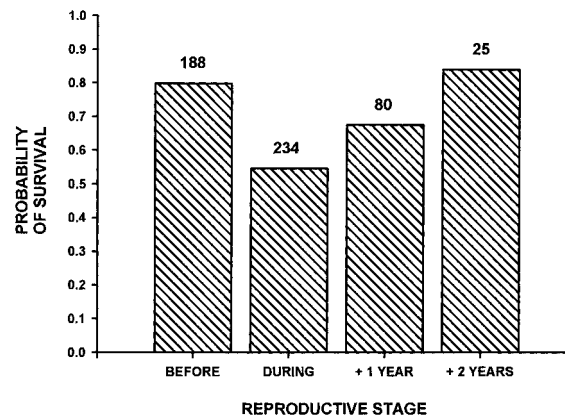
Figure 2. Survival rates of adult female vipers (*Vipera aspis*) in each year of their reproductive cycle. 'Before' = pre-reproductive females; 'during' refers to the year when offspring are produced; '+1 year' means the year following litter production; '+2 years' means the subsequent 12-month period. Sample size are indicated above each bar. See text for explanation of criteria used, and statistical tests on these data.

size. This delay is clearly used to build up energy reserves (Fig. 1); a female that was an income breeder would not need to delay for this additional year, and so would not pay this cost. Females in this phase comprise two of the groups in Figure 2: pre-reproductive animals, and females 2 years post-partum. For both groups, annual survival rates were approximately 82%. Assuming for simplicity that females differ only in the length of their cycle, the pre-breeding cost averaged an additional 18% probability of mortality for a female viper with a 3-year reproductive cycle. For a female with a 4-year cycle (also common in our study population), this component of cost is paid in two successive years as energy stores are laid down. The total additional risk for such a female is thus 33% ($=1.0 - [0.82 \times 0.82]$). Much of this additional mortality may not be a direct consequence of reproductive-related activities such as increased foraging effort, but may be due to random mortality that also affects immature individuals and adult males. Nonetheless, the mortality is experienced because of the need to delay reproduction until females reach the reproductive threshold, and thus can legitimately be considered as a 'cost' of this delay.

(2) *Breeding cost.* In the year that they initiated vitellogenesis, females experienced an annual survival rate of only 54%. Thus, the cost of the activities directly associated with offspring production (e.g., mating, gestation, parturition) averaged 46%. As above, we note that some component of this mortality risk may be unrelated to reproductive activities, but nonetheless comprises part of the 'costs' that are paid during the reproductive year.

(3) *Post-breeding cost.* Females experienced high mortality in the year immediately following parturition (Fig. 2; 67% survival = 33% cost: note above
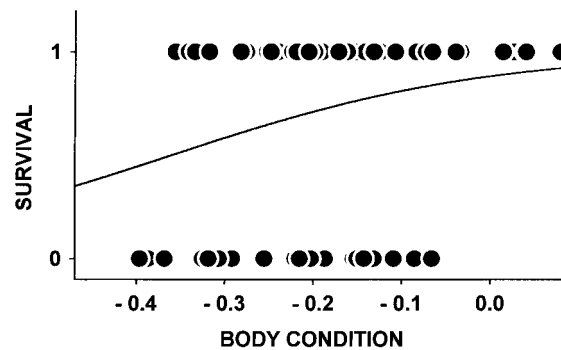
Figure 3. Logistic regression of a female viper's probability of survival in the twelve months following her production of a litter, as a function of her post-parturient body condition. Body condition was calculated as the residual score from the general linear regression of ln-transformed mass versus snout-vent length for all females within the population; almost all values are negative because post-parturient females are always in much poorer body condition than are other (pre-reproductive) females. See text for explanation and statistical results.

caveat). Survival rates of female vipers were lower in the immediately post-parturient year than in other 'non-reproductive' years (Fig. 2; comparing survival rates in the years immediately preceding *vs.* following the 'reproductive' year: $\chi^2 = 4.7$, $df = 1$, $p = 0.031$). This difference supports the notion that there are mortality risks associated with reproducing, that are not manifested until long after the litter is produced.

To further test this proposition, we can compare a female's probability of survival in that post-parturient year, to her body condition (residual score from the linear regression of ln-transformed mass to SVL) immediately following parturition in the preceding year. We used logistic regression for this analysis, because the dependent variable (survived *vs.* died) is a dichotomous trait. As predicted, a female's probability of survival in the year after she reproduced was significantly higher if she was in relatively better body condition immediately after giving birth the year before ($\chi^2 = 5.8$, $df = 1$, $p = 0.016$; Fig. 3). This significant association supports the interpretation that mortality in the year after litter production constitutes a delayed (post-breeding) cost of reproduction for female vipers.

Discussion

The central result from our analysis is a very straightforward one: the timescale over which we measure costs of reproduction needs to reflect the timescale over which an animal engages in activities that support that reproductive bout. In capital-breeding species, that timescale may well be very much greater than the

actual period over which overt 'reproduction' (production of offspring) occurs. The extended timescale reflects two factors: a longer pre-reproductive period of energy-gathering, and a longer post-reproductive period when effects of reproductive activities are manifested. Interspecific comparisons based on shorter timescales are likely to be misleading if they compare different components of reproductive cost of one kind of organism (e.g., an avian income-breeder) *vs.* the other (a reptilian capital-breeder).

Previous theoretical treatments have identified the importance of this distinction between pre- and post-breeding costs of reproduction for understanding the evolution of reproductive tactics (Sibly and Callow, 1984; Stearns, 1992; Jönsson *et al.*, 1995a, b; Jönsson, 1997). Our data provide strong empirical support for the assumptions that underpin these models, especially those proposed by Jönsson *et al.* (1995a, b). Thus, our data support the idea that optimal reproductive investment should increase when costs experienced late in the reproductive cycle (breeding plus post-breeding costs) are higher than pre-breeding costs. This situation is exactly the one that we have found in the asp viper (see above results and Bonnet *et al.*, 1994).

Our results also allow us to develop this idea further. The evolution of semelparity can be viewed as a consequence of extreme capital breeding tactics, where most of the maternal somatic resources are invested during a single reproductive bout (Bonnet *et al.*, 1998). Semelparity may be favoured when the sum of survival costs measured over a long timescale (3–4 years on average in our study model) are particularly high. This extreme reproductive tactic, observed almost exclusively in ecthotherms, may also be associated with components of reproductive costs that are independent of fecundity (Bull and Shine, 1979; Olson *et al.*, 2000).

In the case of female aspic vipers, costs of reproduction are so high that most females produce only a single litter during their lifetime. Especially if energy acquisition is required over a period of two years rather than one, the annual survival rate of females is so low (Fig. 2) that few females survive long enough to produce a second litter. Although the survival cost in the year of litter production is < 50%, the additional risks due to pre-breeding mortality (18–33%, depending on cycle length) and post-breeding mortality (33%) combine to make semelparity the norm for female vipers in our study population (Naulleau *et al.*, in prep.). This result emphasises the importance of understanding all components of reproductive costs, not simply those that are paid during the actual 'reproductive' bout. In our study animals, these additional components (mostly post-breeding costs) sum to at least as high a cost as the overt mortality risk experienced by a female in the year in which she produces offspring.

More generally, methodologies for measurement of costs need to be evaluated carefully before comparisons can be made. This caveat extends to

particular techniques as well as to timescales. For example, the popular technique of assessing avian costs through clutch-size manipulation after laying does not incorporate any effects of the additional clutch size on maternal mobility prior to laying. Such effects may well occur in birds (e.g., Lee *et al.*, 1996), and are believed to be an important component of the total costs experienced by some reptiles (e.g., Shine, 1980; Seigel *et al.*, 1987; Sinervo and DeNardo, 1996).

Similarly, our logistic regression detected a significant mortality cost of reproduction associated with maternal body condition after parturition (see above, and Fig. 3). Post-parturient condition also affects maternal survival in two other species of snakes that are partly sympatric with aspic vipers, but in both cases the correlation is apparent in the few months following parturition (*Vipera berus* – Madsen and Shine, 1993; *Coronella austriaca* – Luiselli *et al.*, 1996). No such link is apparent within aspic vipers over that period (post-partum body condition did not affect a female viper's probability of survival to the next season; $n = 93$, $p = 0.31$ – Naulleau *et al.*, in prep.): the survival cost of lowered maternal condition is only seen over the ensuing 12 months. This contrast suggests that even when species display similar relationships between reproductive effort and cost, the taxa may differ in the timescale over which such effects are manifested.

These kinds of complications do not invalidate broad-scale comparisons of costs: indeed, we enthusiastically endorse attempts to do so. There will be many species that are phylogenetically distant from each other, but for which the form and timescale of costs are sufficiently similar that comparisons are relatively straightforward. For example, although ectothermy predisposes animals to capital-breeding, there are many income-breeders within this group also (e.g., short-lived lizards, James and Whitford, 1994). Similarly, some endotherms rely upon stored 'capital' for reproduction (e.g., Cherel, 1995; Cherel *et al.*, 1993) and some endotherms experience relatively delayed, long-term survival costs (Daan *et al.*, 1996; McCleery *et al.*, 1996). Thus, there are many opportunities to carry out appropriate comparisons among suitably-matched groups of species. Many of the comparisons that we have made (such as capital *vs.* income, or timescales for energy acquisition in birds *vs.* snakes) are clearly continuous rather than dichotomies. Future research could usefully quantify such timescales.

Given the logistical difficulties of the kind discussed here, however, it may also be worth investigating the massive potential of intrageneric (and even, intraspecific) comparisons to clarify costs of alternative life-history traits. For example, many reptile lineages display variation in traits (such as mean body sizes, degrees of sexual size dimorphism, reproductive mode) at these levels (Fitch, 1981; Blackburn, 1982, 1985). This diversity, among taxa that are otherwise very similar, offers a particularly powerful opportunity to

characterise and quantify the costs associated with phylogenetic shifts in traits of interest. Ultimately, such comparisons may be more revealing than those made between taxa that differ so substantially in the form and timescale of costs that it is difficult to overcome the confounding variables involved.

Acknowledgements

References

Bell, G. (1980) The costs of reproduction and their consequences. *American Naturalist* **116**, 45–76.

Bell, G. and Koufopanou, V. (1986) The cost of reproduction. In: R. Dawkins and M. Ridley (eds) *Oxford Surveys in Evolutionary Biology*. Oxford University Press, Oxford, pp. 83–131.

Blackburn, D.G. (1982) Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphibia-Reptilia* **3**, 185–205.

Blackburn, D.G. (1985) Evolutionary origins of viviparity in the Reptilia. II. Serpentes, Amphisbaenia, and Icthyosauria. *Amphibia-Reptilia* **6**, 259–291.

Bonnet, X., Naulleau, G. and Mauget, R. (1994) The influence of body condition on 17-β estradiol levels in relation to vitellogenesis in female *Vipera aspis* (Reptilia, Viperidae). *General and Comparative Endocrinology* **93**, 424–437.

Bonnet, X. and Naulleau, G. (1996) Catchability in snakes: consequences on breeding frequency estimates. *Canadian Journal of Zoology* **74**, 233–239.

Bonnet, X., Bradshaw, D. and Shine, R. (1998) Capital versus income breeding: an ectothermic perspective. *Oikos* **83**, 333–342.

Bonnet, X., Naulleau, G., Shine, R. and Lourdais, O. (2000) Reproductive *versus* ecological advantages to larger body size in female snakes (*Vipera aspis*). *Oikos* **89**, 509–518.

Bull, J.J. and Shine, R. (1979) Iteroparous animals that skip opportunities for reproduction. *American Naturalist* **114**, 296–316.

Cherel, Y. (1995) Nutrient reserve storage, energetics, and food consumption during the prebreeding and premoulting foraging periods of king penguins. *Polar Biology* **15**, 209–214.

Cherel, Y., Charassin, J.B. and Handrich, Y. (1993) Comparison of body reserves build-up in prefasting chicks and adults of king penguins (*Aptenodytes patagonicus*). *Physiological Zoology* **66**, 750–770.

Cichon, M., Olejniczak, P. and Gustafsson, L. (1998) The effect of body condition on the cost of reproduction in female collared flycatchers *Ficedula albicollis*. *Ibis* **140**, 128–130.

Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*. Princeton University Press, Princeton, New Jersey.

Daan, S., Deerenberg, C. and Dijkstra, C. (1996) Increased daily work precipitates natural death in the kestrel. *Journal of Animal Ecology* **65**, 539–544.

Drent, R.H. and Daan, S. (1980) The prudent parent: energetic adjustments in avian breeding. In: H. Klomp and J.W. Woldendorp (eds) *The Integrated Study of Bird Populations*. North-Holland, Amsterdam.

Fitch, H.S. (1981) Sexual size differences in reptiles. *Miscellaneous Publications of the Museum of Natural History, University of Kansas* **70**, 1–72.

Gregory, P.T. (1982) Reptilian hibernation. In: C. Gans and F.H. Pough (eds) *Biology of the Reptilia,* Vol. *13*, Academic Press, London, pp. 53–154.

Gustafson, L. and Sutherland, W. (1988) The costs of reproduction in the collared flycatcher *Ficedula albicollis. Nature* **335**, 813–815.

James, C.D. and Whitford, W.G. (1994) An experimental study of phenotypic plasticity in the clutch size of a lizard. *Oikos* **70**, 49–56.

Jönsson, K.I., Tuomi, J. and Järemo J. (1995a) Reproductive effort tactics: balancing pre- and postbreeding costs of reproduction. *Oikos* **74**, 35–44.

Jönsson, K.I., Tuomi, J. and Järemo J. (1995b) On the consequences of pre- and postbreeding costs in the evolution of reproductive effort tactics. *Écoscience* **2**, 311–320.

Jönsson, K.I. (1997) Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos* **78**, 57–66.

Lee, S.J., Witter, M.S., Cuthill, I.C. and Goldsmith, A.R. (1996) Reduction in escape performance as a cost of reproduction in gravid starlings, *Sturnus vulgaris. Proceedings of the Royal Society, London B* **263**, 619–623.

Luiselli, L., Capula, M. and Shine, R. (1996) Reproductive output, costs of reproduction, and ecology of the smooth snake, *Coronella austriaca*, in the eastern Italian Alps. *Oecologia* **106**, 100–110.

Madsen, T. and Shine, R. (1993) Costs of reproduction in a population of European adders. *Oecologia* **94**, 488–495.

McCleery, R.H., Clobert, J., Julliard, R. and Perrins, C.M. (1996) Nest predation and delayed cost of reproduction in the great tit. *Journal of Animal Ecology* **65**, 96–104.

Naulleau, G. and Bonnet, X. (1996) Body condition threshold for breeding in a viviparous snake. *Oecologia* **107**, 301–306.

Naulleau, G., Bonnet, X. and Duret, S. (1996) Déplacements et domaines vitaux des femelles reproductrices de vipères aspic *Vipera aspis* (Reptilia, Viperidae) dans le centre ouest de la France. *Bulletin de la Société Herpétologique de France* **78**, 5–18.

Nilsson, J.A. and Svensson, E. (1996) The cost of reproduction: a new link between current reproductive effort and future reproductive success. *Proceedings of the Royal Society, London B* **263**, 711–714.

Nur, N. (1988) The costs of reproduction in birds: an examination of the evidence. *Ardea* **76**, 155–168.

Olsson, M., Shine, R. and Bak-Olsson E. (2000) Locomotor impairment of gravid lizards: is the burden physical or physiological? *Journal of Evolutionary Biology* **13**, 263–268.

Pough, F.H. (1980) The advantages of ectothermy for tetropods. *American Naturalist* **115**, 92–112.

Saint Girons, H. (1952) Ecologie et éthologie des vipères de France. *Annales des Sciences Naturelles, Zoologie* **14**, 263–343.

Saint Girons, H. (1957a) Croissance et fécondité de *Vipera aspis* (L). *Vie et Milieu* **8**, 265–286.

Saint Girons, H. (1957b) Le cycle sexuel chez *Vipera aspis* (L). dans l'ouest de la France. *Bulletin Biologique de France et de Belgique* **91**, 284–350.

Schaffer, W.M. (1974) Optimal reproductive effort in fluctuating environments. *American Naturalist* **964**, 783–900.

Seigel, R.A., Huggins, M.M. and Ford, N.B. (1987) Reduction in locomotor ability as a cost of reproduction in snakes. *Oecologia* **73**, 481–485.

Shine, R. (1980) Costs of reproduction in reptiles. *Oecologia* **46**, 92–100.

Shine, R. and Schwarzkopf, L. (1992) The evolution of reproductive effort in lizards and snakes. *Evolution* **46**, 62–75.

Sibly, R.M. and Calow, P. (1984) Direct and absorption costing in the evolution of life cycles. *Journal of Theoretical Biology* **111**, 463–473.

Sinervo, B. and DeNardo, D.F. (1996) Costs of reproduction in the wild: path analysis of natural selection and experimental tests of causation. *Evolution* **50**, 1299–1313.

Stearns, S.C. (1992) The evolution of life histories. Oxford University Press, Oxford.

Tombre, I.M. and Erikstad, K.E. (1996) An experimental study of incubation effort in high-arctic barnacle geese. *Journal of Animal Ecology* **65**, 325–331.

Williams, G.C. (1966a) *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton University Press, New Jersey.

Williams, G.C. (1966b) Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* **100**, 687–690.

Winkler, D.W. and Wallin, K. (1987) Offspring size and number: a life history model linking effort per offspring and total effort. *American Naturalist* **129**, 708–720.