

From Physiology to Fitness: The Costs of a Defensive Adaptation in Rattlesnakes

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Accepted 7/8/2005; Electronically Published 11/14/2005

ABSTRACT

The costs of using and maintaining presumed adaptations are unknown for most animals. Energetically expensive traits, such as some agonistic and antipredator behaviors in animals, may incur trade-offs with other aspects of an animal's life history, such as feeding and reproduction. However, infrequent and brief use may reduce the costs of vigorous behaviors. The shaker muscles in the tails of rattlesnakes are an excellent system for studying the potential costs of a specialized defensive system. The high energetic cost of rattling may increase feeding requirements or use energy that could otherwise be available for reproduction. I used energetic modeling to test whether the cost of rattling in western diamond-backed rattlesnakes (*Crotalus atrox*) can be high enough to increase feeding demands or reduce fecundity and fitness. Only very frequent and prolonged rattling would increase feeding needs and perhaps reduce fecundity to some degree. Typically, rattling probably incurs very low costs to feeding, reproduction, and hence fitness. These and other results suggest that many seemingly expensive adaptations may have minimal costs to energy budgets, reproduction, and fitness.

Introduction

The energetic and fitness consequences of presumed adaptations are rarely known and are often assumed rather than measured (Townsend and Calow 1981; McKnab 2002). Quantifying the energetic costs of adaptations is a crucial step in assessing whether there is a life history trade-off in which the use of a particular trait negatively affects other aspects of an animal's biology (Reznick 1985; van Noordwijk and de Jong 1986; Stearns 1989; Zera and Harshman 2001). For example, energy

spent on specialized agonistic or antipredator behaviors must be regained through increased feeding and may reduce the amount of energy available for reproduction. However, because of the variable and often brief occurrence of many specialized behaviors in animals, few studies have measured their energetic or reproductive costs (e.g., Bennett and Houck 1983; Riechert 1988; Smith and Taylor 1993; Hack 1997; Cleveland 1999).

The rattling system of rattlesnakes is an excellent study system for assessing the potential costs of a specialized defensive behavior to feeding and reproduction. The rattling system is a complex defensive adaptation that generates sounds in order to deter potentially dangerous animals (Klauber 1972; Greene 1988). Sound production by animals typically requires sustaining extremely fast movements that incur high energetic costs (Conley and Lindstedt 1998; Rome and Lindstedt 1998). Rattling is one of the fastest sustainable vertebrate movements and is produced by specialized shaker muscles in the tail that have extremely high aerobic capacity, mass-specific metabolic rates, and endurance (Schaeffer et al. 1996). The mass-specific metabolic rate of shaker muscle exceeds the maximum rates reported for nearly all vertebrates (Schaeffer et al. 1996). Furthermore, Schaeffer et al. (1996) reported that shaker muscle metabolism during rattling approaches the muscle mass-specific metabolism in one of the most aerobic mammals, the pronghorn antelope. Rattling is used only in defensive contexts (Klauber 1972; Greene 1988) and therefore probably does not increase the risk of predation. These results suggest that the cost of rattling may affect rattlesnake energy budgets and ecology (Moon et al. 2002b). Specifically, because rattlesnakes move and feed infrequently, and because reproduction in females is typically energy limited (e.g., Seigel and Ford 1987; Beck 1995; Gregory et al. 1999; Beaupre 2002), a high annual cost of rattling may increase feeding demands or reduce the energy available for growth and reproduction. These effects in turn may increase the risk of mortality (Bonnet et al. 1999; Madsen and Shine 2000). If these effects do occur, then the survival benefits incurred by the specialized defensive system may be associated with subsequent and complex costs.

The impact of rattling on an individual's energy budget can be modeled by integrating the known energetic cost of rattling over a wide range of bout frequencies and durations and then relating the cost to the animal's annual energy budget. In this study, I used energetic modeling to test whether the cost of rattling in western diamond-backed rattlesnakes (*Crotalus atrox*) can become high enough to increase feeding demand or decrease female reproductive output, which is a key component

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Table 1: Metabolic rates (MR) and annual energy budgets of rattlesnakes

Species	Size (g)	Active-Season MR (kJ/d)	MR Estimated for a 300-g Individual (kJ/d)	Annual Energy Budget for a 300-g Individual (kJ) ^a
<i>Crotalus atrox</i>	300	4.46 ^b	4.46	1,103
<i>C. atrox</i>	312.5	4.79 ^c	4.66	1,168
<i>C. cerastes</i>	125	4.83 ^d	5.64	1,391
<i>C. lepidus</i>	114.9	5.03 ^e	6.24	1,530

Note. MR values for a 300-g individual were extrapolated using the mean MRs and masses reported in the original studies and a scaling exponent of 0.76 (Bennett and Dawson 1976; Andrews and Pough 1985).

^a Represents annual energy budget, without rattling, for 229 d of activity and 136 d of inactivity (presumably hibernation), as reported for *C. atrox* in the Sonoran Desert of southern Arizona by Beck (1995). MR for hibernation estimated for a 300-g snake using the data in Table 2 of Secor and Nagy (1994).

^b Calculated using the oxygen consumption reported by Beck (1995) and a conversion factor of 19.86 J/mL O₂ (Gessaman and Nagy 1988; McCue and Lillywhite 2002).

^c Calculated using the equations in Table 3 of Beaupre and Duvall (1998) and a conversion factor of 19.86 J/mL O₂.

^d From the data in Table 2 of Secor and Nagy (1994).

^e Grand mean value from Table 2 of Beaupre (1996).

of fitness. Thus, I quantify the potential energetic and reproductive costs of a highly specialized defensive adaptation.

Material and Methods

This study involved four analytical steps that integrated the results of published research, which I summarize here and describe in detail below. First, I estimated annual energy budgets, excluding rattling, for a 300-g western diamond-backed rattlesnake (*Crotalus atrox*). Second, I obtained the metabolic cost of rattling and used it in simple energetic modeling to determine the annual cost of rattling for a wide range of rattling bout frequencies and durations. Third, I used values for the energy obtained from rattlesnake prey to estimate how much feeding would be required to pay for the annual cost of rattling. Finally, I assessed whether the cost of rattling can be high enough to reduce brood size.

Energy Budgets

Energy use in rattlesnakes varies among populations, individuals of different ages and sizes, and environmental conditions (Beaupre 1993). Therefore, I modeled how the cost of rattling affects the annual energy budget of western diamond-backed rattlesnakes in the Sonoran Desert of Arizona, where the seasonal activity patterns, energetics, and cost of rattling have been studied in this species (Beck 1995; Schaeffer et al. 1996; Beaupre and Duvall 1998). Specifically, I estimated the annual energy budgets for western diamond-backed rattlesnakes based on metabolic rates of other rattlesnakes that were derived from laboratory measurements of oxygen consumption (Beck 1995; Beaupre and Duvall 1998) and field measurements of carbon dioxide production using doubly labeled water (Secor and Nagy 1994; Beaupre 1996). For the laboratory data, I converted all values of oxygen consumption to joules assuming a respiratory

quotient of 0.72, which gives a conversion factor of 19.86 J/mL O₂ (Gessaman and Nagy 1988; McCue and Lillywhite 2002). Note that the field metabolic rates probably include some rattling, which may cause some error in my analysis; however, infrequent rattling would keep the error small. Extrapolating the metabolic rate and energy budget of western diamond-backed rattlesnakes from results for other rattlesnakes is possible because no significant differences in mass-independent metabolic rates have been detected among species or between males and nonreproductive females (Beaupre 1993; Beaupre and Duvall 1998).

I started with the daily metabolic rate (or with the equations for calculating it) and the average body mass reported in each study and used a scaling exponent of 0.76 (Bennett and Dawson 1976; Andrews and Pough 1985) to estimate the value for a 300-g individual (Table 1). In calculating the annual energy budgets, I assumed 229 d of activity and 136 d of winter inactivity, as reported by Beck (1995). I assumed that the winter inactivity was caused by hibernation. I used the entire annual energy budgets from Beck (1995) and Secor and Nagy (1994) because they included both activity and hibernation. For the other studies (Beaupre 1996; Beaupre and Duvall 1998), I used active-season data and added estimates of the metabolic rate during hibernation based on data from Secor and Nagy (1994).

Cost of Rattling

During rattling at 30°C (which approximates the mean activity temperature of 29°C reported by Beck [1995]), western diamond-backed rattlesnakes use 6 mL O₂/kg body mass/min (Schaeffer et al. 1996). I converted this metabolic rate to units of energy as described above and then estimated the cost of rattling for an entire activity season. Because the frequency and duration of rattling bouts in the wild have not been reported

for any species of rattlesnake, I modeled a wide range of rattling bout frequencies and durations. Specifically, for an entire activity season, I summed the duration of rattling that would result from one bout of rattling per day to one bout every 10 d (0.1 bout/d) and for 1–10 min of rattling per bout. From the total rattling time, I calculated the energy used for rattling by a 300-g snake.

Feeding

To estimate the mass of prey that would be required to supply the energy for rattling, I divided the total annual cost of rattling by the net energy assimilated from rodent prey. I estimated the net energy assimilation by starting with the metabolizable energy yield of rodents (4,770 J/g wet mass; Secor and Nagy 1994) and then subtracting 12% for the specific dynamic action in medium-sized to large rattlesnakes (Andrade et al. 1997; Zaidan and Beaupre 2003), which represents the fraction of assimilated energy spent on digestion.

Reproduction

In central Arizona, female western diamond-backed rattlesnakes mature at a mass of approximately 240 g and rarely grow larger than 500 g in nonreproductive mass (Beaupre and Duvall 1998; Beaupre et al. 1998). Very little energy is spent on growth in mature females (Beaupre and Duvall 1998). Female rattlesnakes allocate energy to reproduction (vitellogenesis) over approximately 240 d encompassing parts of two activity seasons (Aldridge and Duvall 2002; Rosen and Goldberg 2002). Furthermore, female rattlesnakes are not known to move much or feed during gestation and instead function solely on stored energy (e.g., Seigel and Ford 1987; Macartney and Gregory 1988; Graves and Duvall 1993, 1995; Beck 1995; Gregory et al. 1999; Beaupre 2002). There is evidence that feeding occurs during vitellogenesis and contributes to reproductive effort in the aspic viper, *Vipera aspis* (Bonnet et al. 2001; Lourdaïs et al. 2002, 2003), which has similar reproductive biology to rattlesnakes, but it remains unclear whether this occurs in rattlesnakes. Therefore, energy spent rattling in mature snakes may directly reduce the energy available for reproduction. I tested whether the cost of rattling can be high enough to reduce a female's fecundity.

The amount of energy contained in a neonate can be determined by multiplying its mass by a neonate energy density of 27.24 kJ/g dry mass (Vitt 1978) and a dry mass content of 25% (Beaupre 2002). Neonatal western diamond-backed rattlesnakes in Arizona have an average mass of 20 g (Rosen and Goldberg 2002) and therefore contain 136 kJ of energy. The amount of energy required to produce 136 kJ of offspring can be calculated by dividing this energy content by a biomass production efficiency of 0.6 (which means that 1 kJ of energy can be converted into 0.6 kJ of tissue; Beaupre 2002). It would

take 227 kJ of energy from the mother to produce the 136 kJ of energy contained in one 20-g offspring. By dividing the annual cost of rattling by the energy required to produce each gram of neonate, I calculated the maximum possible reduction in brood mass that can result from energy spent rattling rather than reproducing.

In Arizona, the average western diamond-backed rattlesnake brood comprises seven offspring (Rosen and Goldberg 2002). Therefore, an average brood has a mass of approximately 140 g. Throughout the range of this species, brood size varies from two to 25 offspring (Ernst and Ernst 2002), presumably in part because of differences in female size. Because I am modeling energetics of approximately average-sized females (300 g) in Arizona, I estimated the maximum percentage by which broods of two to 10 offspring could be reduced in mass as a result of the annual cost of rattling. This way of estimating the costs of rattling to fecundity may slightly overestimate the maximum effect because some energy spent rattling may be diverted away from daily activity rather than reproduction.

Maternal energy is available evenly to an entire brood of developing follicles, but individual follicles appear to compete for it with variable success (Jones 1978; Sinervo and Licht 1991a, 1991b; Sinervo 1994). Follicles that do not obtain enough energy degenerate, even at a relatively advanced stage of development (Jones 1978). Therefore, energy diverted away from reproduction may reduce offspring size evenly or unevenly. In lizards, hatchlings must attain some minimal size to be viable (Bauwens and Diaz-Uriarte 1997); this seems likely to be true for snakes as well. Neonatal western diamond-backed rattlesnakes vary in size by approximately 25% (Klauber 1937). Therefore, I assumed that offspring more than 25% smaller than average would be unlikely to survive, which would reduce the mother's fecundity and hence possibly reduce her fitness.

I inferred two levels of fecundity effects, depending upon the maximum possible reduction in fecundity. I inferred a small effect if energy spent rattling could lead to a 25% or greater reduction in the mass of one offspring, which would render that offspring unviable. Although loss of one offspring per brood may have a large impact on the fitness of animals such as rattlesnakes that mature late and reproduce infrequently, it is also likely that energy remaining after the loss of that offspring (up to 75% of the energy that would have been allocated to it) would be reallocated to the other offspring. Therefore, the remaining offspring may increase in size and survivorship, which could partially compensate for the reduced output of that reproductive cycle. I inferred a large effect on fecundity if energy spent rattling could lead to at least a 25% reduction in total brood mass, which could eliminate the entire brood.

This approach of inferring the effects of fecundity on fitness may be oversimplified, but in the absence of specific data on how variation in size affects offspring viability, it provides a quantitative starting point for this kind of analysis. These estimated thresholds are also conservative because they would

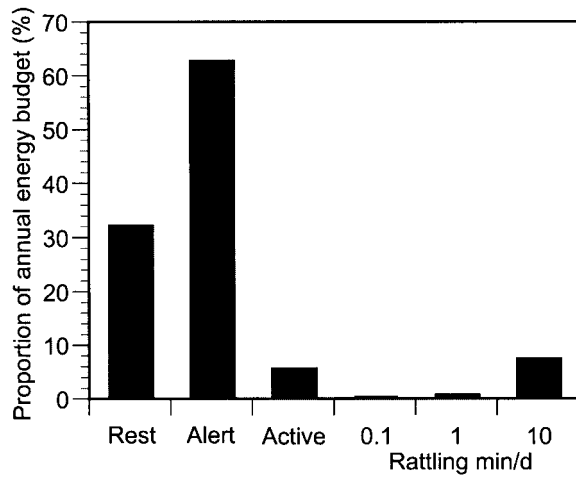


Figure 1. Annual energetic costs of four behaviors in a 300-g western diamond-backed rattlesnake (*Crotalus atrox*) in southern Arizona, expressed as a percentage of the lowest estimated annual energy budget without rattling (derived from Beck 1995 and this study). Three different rates of rattling are shown for comparison with nonrattling behaviors. “Active” snakes were moving, “alert” snakes were stationary but kept their heads tilted upward and readily extended the tongue when presented with minimal stimuli, and “resting” snakes were not active or alert. Under most circumstances, the cost of rattling is probably a very small component of the annual energy budget.

lead to an inference of reduced fitness only for relatively large reductions in reproductive output.

Results

Although the mass-specific metabolic rate of active shaker muscle is very high, the annual cost of rattling is only a small fraction of the total annual energy budget of rattlesnakes, even with frequent and prolonged rattling. The consequences of this small annual cost of rattling vary with brood size but are unlikely to be important for any brood size.

In a 300-g western diamond-backed rattlesnake, the annual

energy budget may vary from approximately 1,100 to 1,500 kJ without rattling (Table 1). This budget could be balanced by eating 263–365 g of rodent prey, which is equivalent to 88%–122% of the snake’s mass. This much energy could be obtained by eating six to eight meals of 45-g rodents such as kangaroo rats, which are a common prey item of rattlesnakes. For snakes of this size, rattling for 1 min once every 10 d (i.e., 0.1 min/d) throughout the activity season would increase the annual energy budget by only 0.1% (Fig. 1; Table 2). This much energy would require a negligible increase in food intake and could reduce brood mass by less than 0.2% (Fig. 2; Table 2). These effects are much too small to reduce fecundity or fitness for any brood size.

The annual cost of rattling would exceed the cost of active movement (approximately 6% of the annual energy budget estimated by Beck 1995) only when a 300-g snake rattled for 8 min/d throughout the activity season (Table 2). The annual costs of this much rattling could be paid by eating one small mouse or lizard, or they could reduce the total brood mass by approximately 3%–14% (Fig. 2; Table 2). These effects probably are not enough to reduce fecundity or fitness.

The annual cost of rattling would be relatively high if a 300-g snake rattled for 10 min every day of its activity season, although this seems highly unlikely to occur given the low levels of activity in rattlesnakes. The annual cost of rattling would equal the energy obtained from one small mouse and could cause a small to moderate reduction in brood mass (Fig. 2; Table 2). However, these effects still would not exceed the threshold I inferred for a small effect on fecundity. A 300-g rattlesnake would have to rattle very frequently and for long periods every day of the active season to reduce fecundity by one or more offspring (Table 2).

Discussion

Rattling presumably enhances rattlesnake survival by deterring predators and other potentially dangerous animals (Klauber

Table 2: Potential effects of rattling on energy balance and reproduction in average-sized female western diamond-backed rattlesnakes

Time Spent Rattling (min/d)	Annual Cost of Rattling (kJ)	Annual Cost of Rattling (%) ^a	Food Required to Pay Cost of Rattling (g) ^b	Reduction in Brood Mass (g)	Reduction in Brood Mass (%) ^c
.1	.82	.07–.05	.2	.1	.18–.04
8	65.5	5.9–4.3	15.6	5.8	14.4–2.9
10	81.9	7.4–5.4	19.5	7.2	18–3.6
13.9	113.8	10.3–7.4	27.1	10	25.1–5.0
69.4	568.1	51.5–37.1	135.4	50	25.0–125.1

^a Indicates the percentages of the minimum and maximum energy budgets without rattling shown in Table 1.

^b Indicates the mass of mammalian prey required to supply enough energy to pay for the annual cost of rattling.

^c Indicates values for broods of two to 10 offspring.

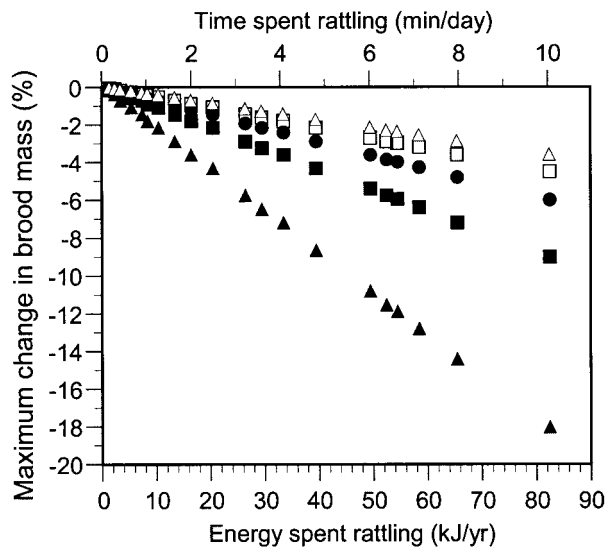


Figure 2. Maximum potential reduction in brood mass resulting from energy spent rattling rather than reproducing in a 300-g western diamond-backed rattlesnake (*Crotalus atrox*). Open triangles = brood size of 10 offspring; open squares = brood size of 8; dots = brood size of 6; solid squares = brood size of 4; solid triangles = brood size of 2. These potential reductions in brood mass probably have very small effects on reproduction and fitness.

1972). The physiological literature suggests that rattling is a very costly defensive behavior (Schaeffer et al. 1996; Conley and Lindstedt 1998; Rome and Lindstedt 1998; Moon et al. 2002b). Rattling in western diamond-backed rattlesnakes (6 mL O_2 /kg/min) costs as much as maximal locomotion (sidewinding) in sidewinder rattlesnakes (6.75 mL O_2 /kg/min; Secor et al. 1992), which may be the fastest and most active rattlesnakes. Furthermore, the mass-specific metabolic rate of shaker muscle exceeds the maximum rates reported for nearly all vertebrates (Schaeffer et al. 1996). These results suggest that the cost of rattling may affect rattlesnake energy budgets and ecology (Moon et al. 2002b).

This analysis shows that rattling probably has negligible effects on annual energy budget, feeding requirements, and reproduction. However, the cost of frequent and prolonged rattling may be important to postpartum females, which typically have poor body condition in capital breeders (Bonnet et al. 1999). Still, under most circumstances, there appears not to be an important trade-off between defense and reproduction in rattlesnakes. These results lead to two questions. What features help reduce the cost of rattling? And do rattlesnakes ever rattle frequently and long enough in the wild to incur substantial energetic and/or fitness costs?

In most animals, the cost of muscle contraction is a major part of the cost of activity. Furthermore, because muscles represent a large fraction of body mass, the cost of contraction is often an important part of the overall energy budget (e.g.,

Taylor and Heglund 1982; Schmidt-Nielsen 1984; Woledge et al. 1985; Alexander 1999). Therefore, an increase in muscle metabolism should lead to an increase in energy expenditure. However, the small mass of shaker muscle and a low cost per contraction help reduce the cost of rattling. The mass of shaker muscle averages 1% of the total body mass in western diamond-backed rattlesnakes (Moon et al. 2002a). Minimal shortening and low force output of shaker muscles help minimize the cost of each contraction so that high-frequency contractions can be sustained (Conley and Lindstedt 1996; Moon et al. 2002a, 2003). Because of these features, even very high mass-specific metabolism during rattling will use only a small absolute amount of energy.

In addition to the physiological features that moderate the cost of rattling, limited use of rattling behavior probably reduces the annual cost of rattling. Although rattlesnakes can rattle continuously for at least 3 h (Martin and Bagby 1972), they appear to rattle only briefly and infrequently in the wild. Pregnant rattlesnakes typically rely on crypsis and escape during initial encounters with potential predators, but they will escalate to rattling and striking if approached closely and touched (Graves 1989). Rattlesnakes in the southwestern United States may rattle in as few as 2%–3% of encounters with humans (Artran 1940, cited in Klauber 1972). Similarly, only 3% of wild pygmy rattlesnakes (*Sistrurus miliarius*) rattle when they are approached and tapped on the head by a person (Rowe et al. 2002).

If western diamond-backed rattlesnakes do rattle only infrequently and briefly, then it would take 33–50 encounters with danger per day to induce a snake to rattle once per day. Considered from another perspective, if a rattlesnake encountered a potentially dangerous animal once every day throughout a 229-d activity season, and it rattled in only 3% of these encounters, then the snake would rattle approximately seven times per year. If a rattlesnake encountered potential danger once every 10 d throughout a 229-d activity season, and it rattled in only 3% of the encounters, then it would rattle only once per year.

The energetic costs of adaptations, such as the rattling system of rattlesnakes, can be partitioned into the costs of use and maintenance. This study indicated that the cost of using the specialized shaker muscles is probably very low. The cost of maintaining the rattling system also appears to be low because the resting metabolism and blood flow in shaker muscle are low (Conley and Lindstedt 1996; Schaeffer et al. 1996; Kemper et al. 2001). Thus, the available data strongly suggest that maintaining and using the specialized rattling system is inexpensive.

Vigorous behaviors that are used briefly and infrequently may incur low costs in diverse animals (e.g., Bennett and Houck 1983; Riechert 1988; Hack 1997; Cleveland 1999; this study). These examples suggest that many seemingly expensive adap-

tations have small costs to energy budgets, reproduction, and fitness.

Acknowledgments

Valuable help during the development of this article was provided by Steven Beaupre, Dale DeNardo, Clay Green, Michele Green, Anthony Herrel, Duncan Irschick, Robert Jaeger, Travis LaDuc, Shannon Martin, Ali Rabatsky, Stephen Secor, Jake Socha, Emily Taylor, Bieke Vanhooydonck, Shawn Vincent, Katherine Wadsworth, and three anonymous reviewers. This research was supported by the University of Louisiana at Lafayette.

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