

Review

The costs of autotomy and regeneration in animals: a review and framework for future research

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Many organisms have the ability to shed an appendage (autotomy) to escape a predator or fouled molting event. Despite its immediate advantage on survivorship, autotomy can have important consequences for locomotion, foraging, survivorship, and/or reproduction. Thus, regeneration is a way that animals alleviate some of the costs associated with losing an appendage. Like autotomy, however, appendage regeneration can have important consequences for a variety of aspects of fitness; in a wide range of amphibians, reptiles, fishes, and arthropods, the allocation of resources to regenerate a lost appendage negatively affects somatic or reproductive growth. Previous research into the costs associated with regeneration has provided a strong framework to explore how trade-offs associated with regeneration may have influenced its evolution. However, all research to date describing the costs and benefits associated with autotomy and regeneration have compared individuals autotomizing and regenerating an appendage with individuals that have never lost an appendage. I suggest that for studies of the evolutionary significance of regeneration, an alternative comparison is between individuals experiencing autotomy without regeneration and individuals experiencing autotomy with regeneration. Future work in this direction promises new insights into the evolution of regenerative tendencies, as well as how regeneration may be influencing animal form and function. *Key words*: autotomy, costs, evolution, regeneration, trade-offs. [*Behav Ecol* 17:857–872 (2006)]

Two thousand and four hundred years ago Aristotle first noticed that lizards could shed and regrow a lost tail. By the 18th century, scientists were actively researching the ability of animals to shed and regenerate lost body parts. Reamur (1710, cited in Emmel 1905, and 1712) was the first to record limb regeneration in insects and crustaceans. Trembly (1740, cited in Emmel 1905) split hydra heads and obtained multi-headed individuals, and Bonnet (1745, cited in Dinsmore 1996) cut worms into multiple pieces, each resulting in a new worm. Most noted of all, Spallanzani (1768, cited in Dinsmore 1996) discovered that tadpoles could produce a new tail; that salamanders could regenerate tails, legs, and/or jaws; and that slugs could even regenerate their head.

Early studies of animal regeneration encompassed 3 basic foci: documenting that regeneration could occur, characterizing abiotic and biotic effects on the speed of regeneration (e.g., Trembly [1740, cited in Emmel 1905] recorded that hydra heads could regenerate faster in warmer weather; and Spallanzani [1768, cited in Dinsmore 1996] showed that nutrient limitation could alter rates of regeneration), and exploring how regeneration occurs at the developmental/physiological level. In 1712, Reamur suggested that small eggs existed underneath a lost leg, and once that leg was removed, these eggs would re-create the lost appendage. Plufger (1883, cited in Emmel 1905) suggested that food material was taken

up at the wound surface and organized into the substance of a new leg. Thus, a hundred years before the theory of natural selection, scientists had already begun to explore how animal development could lead to the regenerative growth of a second appendage. Regeneration remained an active focus of biological research through the end of the 1800s and into the early 1900s (for reviews on the early history of regeneration research, see Morgan 1901; Emmel 1905; Dinsmore 1991, 1996).

By the 1960s, the focus of this work had shifted from an emphasis on the regenerative process itself to a broader concern for development in general. The capacity of certain animals to regrow a lost leg or tail was exploited as a powerful tool for biologists to study the fundamental aspects of development, such as wound healing, blastema formation, and cell differentiation/growth. And as a result, we now understand many of the mechanistic details of the regeneration process at the genetic, cellular, tissue, organ, and organismic level. (For general reviews, see Goss 1969; Wallace 1981; for taxon-specific reviews, see—lizards: Bellairs and Bryant 1985; amphibians: Scadding 1977, 1980; Tsonis 1991; Brockes 1997; Nye et al. 2003; fishes: Wagner and Misof 1992; Becerra et al. 1996; crustaceans: Bliss 1960; Skinner 1985; Juanes and Smith 1995; Marsh and Theisen 1999; Hopkins 2001; echinoderms: Dubois and Ameye 2001; insects: Needham 1965; Bulliere D and Bulliere F 1985; spiders: Vollrath 1990.)

Regeneration research continues today to advance our understanding of animal development. What has been secondary in this process is an interest in the morphological and ecological implications of regeneration for the organisms themselves. Why do select species retain the capacity to shed and regrow body parts, whereas most others do not, and what are the costs and benefits to these individuals of this phenomenon?

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Ironically, despite being one of the oldest studied developmental phenomena, regeneration is not often considered in the context of natural selection and evolution. This is particularly striking, given that numerous studies show that there can be important trade-offs with the regrowth of an appendage. In this paper, I review existing studies that address the performance and/or fitness consequences of autotomy and regeneration, and I focus primarily on the costs associated with this process. In addition, this review revealed an important gap with regard to the evolution of regenerative abilities, and I end this paper by proposing alternative ways to study the fitness consequences of animal regeneration.

Ungulate antlers, turtle shells, crocodilian jaws, bat wings, and snail penises have all been shown to regenerate (Bellairs and Bryant 1985; Goss 1987; Dytham et al. 1996). In a few taxa, regeneration can even serve as a means of asexual reproduction (e.g., poriferans, earthworms, and asteroids). However, the most common forms of regeneration—and those that are best characterized developmentally—all involve appendages, such as legs and tails, and I focus on these for the remainder of this review. I first focus on the process of appendage loss (autotomy) and then discuss the process of secondary regrowth (regeneration).

AUTOTOMY

A discussion of appendage regeneration is incomplete without first addressing the subject of autotomy. The term was originally introduced by Fredericq (1892) (originally called *autotomie*) and describes the reflex severance of an appendage without aid from any source other than from the severed appendage. An example would be the voluntary severance of a lizard tail to distract a predator that has not yet attacked. There are 3 other closely related terms defined by various authors in the early 1900s (reviewed by Wood FD and Wood HE 1932). “Autopasy” (also spelt *autospasy*) refers to a situation where an outside agent is responsible for the severance of an appendage at a preformed breakage plane (e.g., the loss of limb to a predator who has grasped it). “Autotilly,” similar to autopasy, occurs when the animal itself removes an appendage with the assistance of its mouthparts or other legs. “Autophage” refers to the act of consuming a shed appendage usually, but not always, after severance from the remainder of the animal (e.g., some lizards: Judd 1955; Grant 1957; Clark 1969; insects: TL Maginnis, personal observation; and eels: George 1978). “Appendotomy” was introduced by Woodruff (1937) as an attempt to encompass all 4 of the previous definitions, but this term has not become popular. Despite the discrete situations described above, “autotomy,” as it is used in current literature, can refer to 1) the reflexive loss of an appendage at a preformed breakage plane (e.g., the herpetology literature), 2) the loss of an appendage at a preformed breakage plane (e.g., the arthropod literature), or 3) the general loss of an appendage with no preformed breakage plane (e.g., the fish and amphibian literature). For this review, I define autotomy to simply mean appendage loss (with no implication of mechanism) so as to include and discuss a breadth of taxa (for reviews on autotomy, see McVean 1975, 1982; Wilkie 2001).

Benefits of autotomy

As hinted by the various definitions of autotomy, there are multiple benefits associated with the ability to shed an appendage. The most prevalent is predation avoidance, which can take 1 of 2 forms depending on the species: a limb or tail may be shed after it has been clasped by a predator or these structures may be shed preemptively as a predator approaches. Shed limbs in these latter examples can often con-

tinue to move or to release toxic substances after they have been separated, and these motile appendages can serve as an effective distraction or even as a substitute meal (moving tails of lizards: Cooper et al. 2004; moving limbs of octopuses: Norman and Finn 2001; substance release in sea slugs: Miller and Byrne 2000). Many studies have shown that autotomy in the face of a predator can improve the immediate survivorship of an individual (Robinson et al. 1970; Dial and Fitzpatrick 1983a; Daniels et al. 1986; Formanowicz 1990), but the long-term consequences of autotomy have been less well explored. It is likely that postautotomy survival will vary greatly depending on other species-specific methods of predator avoidance, such as aposematic coloration, mimicry, claws/teeth, level of aggression, size of autotomized appendage, and escape speed. (Arnold 1984, 1985).

Survivorship benefits of autotomy as they relate to predation avoidance can take many forms. Predators and/or predation events need not be typical; spider webs, fresh sap flows, limbs that come in contact with toxins/pesticides (Moore and Tabashnik 1989), long limbs stuck in crevasses during foraging (Norman and Finn 2001), legs injected with spider venom (Eisner and Camazine 1983), legs or mouthparts of parasites stuck in a host (Nuttall 1920), tails used as burrow plugs (Arnold 1984), crab legs harvested by fishermen (Bennett 1973), cannibalistic attacks (George 1978), and/or intraspecific competitions (Vitt et al. 1977; Henning 1979; Roth VD and Roth BM 1984) can also create situations where an individual must shed an appendage to survive. In aquatic habitats, autotomy at a preformed breakage plane may be especially advantageous; not only does it facilitate escape from a predator but also the preformed cleavage plane can speed up wound healing, reduce bacterial infection, and minimize potential water-borne cues that could signal the presence of a wounded animal (Zimmer-Faust 1989; Lawrence and Larrain 1994; Juanes and Smith 1995). Interestingly, autotomy in the face of predation can simultaneously permit survival and facilitate predator foraging; earthworm autotomy in response to ant attacks permits the earthworm to survive and benefits the ants because the shed pieces of worm are more easily transported (Dejean et al. 1999).

Most studies that explore the benefits of autotomy concern predation (e.g., autotomy as a mechanism of escape). However, arthropods derive an additional benefit of autotomy through an entirely different form of escape: escape from a fouled molt. All arthropods have their skeleton on the outside of their body, and one inescapable consequence of an exoskeleton is that it must be periodically shed if an animal is to grow to a larger size. Molting is a complex process that involves the formation of a new and pliable exoskeleton inside the existing smaller one. When the new large skeleton is complete, the animal first climbs itself out of the old one and then expands and hardens its new one. Often, when crustaceans, insects, and spiders molt from one stage to the next, appendages become stuck in the old exoskeleton and these body parts must be shed if the organism is to survive (Bedford 1978; Foelix 1982; Robinson et al. 1991; Brock 1999; TL Maginnis, personal observation). Tangled molts can be especially common in species with large, defensive forelimbs (e.g., crabs) or in species with relatively long and slender legs (e.g., stick insects). Clearly, there are multiple survival benefits that can accrue from an animals' ability/capacity to shed a leg or tail. But these benefits do not come without costs.

Costs of autotomy

The most obvious cost of autotomy is the impediment to efficient locomotion that results from the absence of an appendage. Loss of a leg or tail can significantly impair running,

walking, gliding, balance, swimming, diving, and/or underwater propulsion (Ballinger et al. 1979; Ballinger and Tinkle 1979; Punzo 1982; Daniels 1985; Arnold 1985; Brown et al. 1995; Martin and Avery 1998; Cooper et al. 2004). Moreover, impaired locomotor performance can translate into a decreased survivorship or the ability to forage/capture prey or escape from predators (survivorship: Fox and McCoy 2000; foraging: Smith and Hines 1991a; Ramsay et al. 2001; Cooper 2003; predator escape: Dial and Fitzpatrick 1983b; Vitt and Cooper 1986; Formanowicz et al. 1990; Wilson 1992; Smith 1995; Stoks 1999; Downes and Shine 2001). Autotomy may also be particularly detrimental in species where the autotomized limb functioned as predator defense; predators often prefer prey missing their defensive limbs because these individuals are easier to handle during foraging. Both turtles and birds, for example, actively seek autotomized crabs during foraging (Bildstein et al. 1989; Davenport et al. 1992).

Appendage autotomy may impair reproduction as well as survival, and this can occur in a variety of ways. First, appendage loss can affect behaviors associated with sexual selection; males missing tails may be unable to effectively defend territories, burrows, and/or females during male–male competitions (Smith 1992; Mariappan and Balasundaram 2003), and females missing tails may be less “attractive” to males during female choice behaviors (Martin and Salvador 1993b). Second, missing an appendage can affect social interactions; males missing a tail are at a disadvantage in species where tails are used as social signaling badges (Fox and Rostker 1982; Fox et al. 1990; Martin and Salvador 1993a; Althoff and Thompson 1994; Salvador et al. 1995). Finally, losing a tail may directly affect female fecundity. In species where the tail is a primary site of fat storage, loss of the tail also means the loss of acquired nutrients and reserves for reproduction; tailless females lay fewer and/or smaller eggs than tailed females (Smyth 1974; Dial and Fitzpatrick 1981).

Another less well-documented cost associated with autotomy is its effects on behavior. Ground skinks (*Scincella lateralis*; Formanowicz 1990), large Psammomys lizards (*Psammomys algirus*; Martin and Avery 1997), Iberian rock lizards (*Lacerta monticola*; Martin and Salvador 1993a, 1993b), and damselflies (*Lestes sponsa*; Stoks 1999) missing appendages were significantly less active or less aggressive than animals with all their appendages, and this reduction in behavior could likely lead to decreased foraging rates and/or mating opportunities.

In summary, the capacity to shed a body appendage has multiple, immediate advantages principally connected with permitting an individual to escape an otherwise fatal situation. However, once a limb has been lost, animals face numerous challenges resulting from the loss of locomotor or foraging abilities, loss of stored resources, or impaired social and reproductive behavior. Lost legs or tails can come at an even greater expense either if more than one limb is lost at a time (especially in animals that can autotomize up to 75% of their body mass; Ramsay et al. 2001) or if they contain additional morphological features, such as glands, adhesive pads, or sensory structures used in other aspects of behavior or physiology (Bellairs and Bryant 1985; Norman and Finn 2001). Costs associated with autotomy presumably vary significantly depending on which appendage is lost; the function of the appendage; and the relative significance of habitat, age class, sex, and/or condition. Many of the organisms that lose appendages, however, have the ability to regenerate them.

REGENERATION

Regeneration (e.g., the partial or complete replacement of a lost appendage) can offset many of the potential long-term

Table 1
Regenerative tendencies in animals

Class	Number of genera	Number of species	Appendage
Reptilia	44	90	Tail
Amphibia	23	52	Leg, tail
Osteichthyes	34	43	Fin
Crustacea	35	45	Leg
Echinodermata	33	45	Arm
Insecta	38	43	Leg
Arachnida	33	38	Leg

See Appendix for full taxa references and citations.

costs of autotomy. Although regenerative capacities can vary extensively across and within taxa (see Table 1 and Appendix), regenerated appendages are often adequate enough to restore some of the locomotor, foraging, reproductive, and/or metabolic disadvantages the animals were facing with the lost appendage (Fox and Rotsker 1982; Daniels 1984; Fox et al. 1990; Martin and Salvador 1993a, 1993b; Chapple and Swain 2002). Although the benefits of regeneration are obvious, the costs of regrowing a lost appendage are not. In the next section, I review the costs associated with having a regenerated appendage, as well as the costs associated with the regeneration process as they are currently discussed in the literature. As such, costs of regeneration can be placed in 2 categories: performance costs associated with relatively smaller appendages and allocation costs associated with the physiological process of appendage regeneration.

Regeneration: performance costs

Regenerated appendages of lizards and amphibians (Hardy CJ and Hardy CM 1977; Salvador et al. 1996; Fitch 2003), crustaceans (Edwards 1972; Savage et al. 1975; Elner 1980; Weis 1982), fishes (Conant 1970; Becerra et al. 1996; Mari-Beffa et al. 1999), insects (Lüscher 1948; Parvin and Cook 1968; Tanaka and Ross 1989; Karuppanan 1998), and spiders (Vollrath 1990) are often smaller than nonregenerated appendages. The reduction in size can vary from slight (<5%) to extreme (~95%), and these relatively smaller limbs can impair foraging, reproduction, and/or survivorship.

Impaired foraging

Shore crabs (*Carcinus maenas*) with regenerated chelae (the first set of appendages), for example, must choose smaller sized prey, and hence have a lower energy uptake, compared with crabs with normal chelae (Elner 1980). The effects of smaller limbs on foraging may also be indirect, as in the case of the garden spider or the common tick. European garden spiders (*Araneus diadematus*) with regenerated legs build structurally different webs, and webs with different geometry vary in their ability to trap different prey types (Vollrath 1987; Schneider and Vollrath 1998; Krink and Vollrath 1999; Weissman and Vollrath 1999). In the common European tick (*Ixodes ricinus*), regenerated forelimbs had altered sensory organs. These organs are used to detect carbon dioxide emitted from hosts, and it has been suggested that these altered sensory organs would impair a tick's ability to effectively locate hosts (Leonovich and Belozarov 1992).

Impaired reproduction

Smaller appendages specifically due to regeneration can also affect reproduction. Uetz et al. (1996) showed that mating success for male brush-legged wolf spiders (*Schizocosa ocreata*)

with regenerated legs was significantly lower than for males with nonregenerated legs; regenerated legs lacked tufts of hairs used in courtship behaviors, and as a result, these males were less attractive to females. Male large Psammmodromus lizards (*P. algirus*) with regenerated tails had proportionately smaller home ranges, and hence reduced access to females, when compared with males with normal tails (Salvador et al. 1995, 1996). And in shore crabs (*C. maenas*), regenerated chelae (used to grasp the female during mating) significantly reduced reproduction in medium-sized males (interestingly, relatively small and large males experienced only minor reductions in mating success; Sekkelsten 1988). The effects of limb regeneration on reproduction can even be manifested through mate calling/singing. In bush crickets (*Ephippiger ephippiger*), regeneration of a leg can produce proportionately smaller hearing organs on the femur or tibia, and females with regenerated legs are less likely to respond to calling/singing males (Lakes and Mücke 1989).

Impaired survivorship

Regeneration of a lost appendage can also affect survivorship. Wilson (1992) and Fox and McCoy (2000) have shown decreased survivorship in side-blotched lizards (*Uta stansburiana*) regenerating tails based on mark-recapture studies. In studies that have looked at percentages of autotomized and regenerated appendages in natural populations, many demonstrate a significantly lower number of regenerating individuals versus the number of individuals experiencing autotomy (Savage et al. 1975; McVean and Findlay 1979; Liu and Wang 1999; Lysenko et al. 2000). Although never explicitly tested, the decreased rate of individuals regenerating compared with the observed rate of autotomy implies that individuals regenerating an appendage experience a reduced survivorship. However, even in studies where decreased survivorship has been unambiguously documented, the mechanism underlying the reduction in survivorship can remain unclear (e.g., fat storage depletion, reduced locomotor/escape ability, or allocation costs could all contribute to reduced survivorship). This is understandable because limbs and/or tails often serve various functions, yet it is clear that the reduced size of regenerated appendages can affect animal performance at many levels.

Regeneration: allocation costs

In addition to the performance costs associated with reduced appendage size, many studies clearly demonstrate that regeneration can affect somatic or reproductive growth. Regrowth of an appendage requires the allocation of resources that would otherwise have gone to somatic growth or reproduction. That is, the physiological allocation of resources that organisms put into the physical regrowth of a structure, sometimes over half their total energy (Vitt et al. 1977), can translate into trade-offs with measurable ecological consequences for these animals. Allocating energy to appendage regeneration has been shown to affect both development and reproduction.

Altered development

In vertebrates, regeneration may decrease overall growth rate. Juvenile Eastern fence lizards (*Sceloporus undulatus*) and bunchgrass lizards (*Sceloporus scalaris*), for example, grow more slowly if they are in the process of regenerating an autotomized tail (Ballinger and Tinkle 1979). Similar patterns can be found in the side-blotched lizard (*U. stansburiana*); in mark-recapture experiments, hatchlings regenerating tails grew more slowly than hatchlings not regenerating tails (Niewiarowski et al. 1997). Delayed growth could reduce fitness in 2 ways. First, a reduced growth rate could lead to relatively smaller adults with consequences for fecundity,

status, and mating success (Ballinger and Tinkle 1979). Second, a reduced growth rate could add to the total time required for reproductive maturation, increasing the cumulative risk of predation. Extended development could be particularly detrimental in species where early maturity or precise timing of maturity is critical for individual fitness (Ballinger and Tinkle 1979).

In arthropods, regeneration can either accelerate or delay molting (an event necessary to commence the regeneration process). Accelerated molting permits an animal to replace its limb faster, but early molting can have negative consequences for overall growth and body size by truncating the time needed to accumulate resources for appendage regrowth, metamorphosis, and/or reproduction. Limb regeneration in both littoral crabs (*Cyrtograpsus angulatus*: Spivak 1990) and the common crayfish (*Cambarus propinquus*: Zeleny 1905) has been shown to accelerate molting.

In other arthropods, regeneration delays molting. Prolongation of immature stages allows animals extra time to accumulate resources, potentially ameliorating at least some of the allocation costs of appendage regeneration. But delays in molting also mean the animal must survive longer without the appendage and may increase the cumulative risk of predation. Similar to delayed growth in vertebrates, a delay in molting could have extra costs if obtaining a critical adult size or stage is crucial to some other aspect of survival or reproduction. Cellar spiders (*Holocnemus pluchei*: Johnson and Jakob 1999), American lobsters (*Homarus americanus*: Emmel 1907), and edible crabs (*Cancer pagurus*: Bennett 1973) all delay molting in response to regeneration.

Interestingly, the effects of regeneration on growth may vary, as in the case of the freshwater crab (*Paratelphusa hydrodromous*). If a limb is lost and subsequently regenerated during the nonbreeding season, growth can either speed up (to regenerate the limb faster: Devi and Adiyodi 2000) or remain the same (to regenerate the limb at a normal rate: Suma Gupta et al. 1989). That is, during the nonbreeding season, energy is allocated to regeneration. Conversely, if a limb is lost and regenerated during the breeding season, either the animals will not regenerate (Suma Gupta et al. 1989) or growth will be delayed until the animals can acquire sufficient energy to both build up its reproductive organs and regenerate the lost limb (Devi and Adiyodi 2000). This flexibility of allocation between somatic and reproductive growth can occur in males (testicular activity: Suma Gupta et al. 1989) as well as in females (oogenesis: Devi and Adiyodi 2000).

Facultative modulation of the effects of regeneration may reflect on other factors besides the breeding/nonbreeding season, such as the ontogenetic stage at which appendage loss occurs or the number of appendages shed. In the American lobster (*H. americanus*), for example, only limbs autotomized at a certain developmental stage decreased overall growth rate (Emmel 1907; Cheng and Chang 1993). Moreover, the effects of regeneration on growth could depend on the intensity of limb autotomy. In edible crabs (*C. pagurus*: Bennett 1973; Weis 1982), shore crabs (*Hemigrapsus oregonensis* and *Pachygrapsus crassipes*: Kuris and Mager 1990), and common starfish (*Asterias rubens*: Ramsay et al. 2001), severe limb loss reduced growth rate, whereas less severe limb loss did not.

Altered fecundity

Recent studies have also demonstrated that energy allocated to appendage regeneration can come at the expense of fecundity. Female velvet swimming crabs (*Necora puber*: Norman and Jones 1993), plethodontid salamanders (*Batrachoseps attenuatus*: Maiorana 1977), Texas banded geckos (*Coleonyx brevis*: Dial and Fitzpatrick 1981), Australian skinks (*Morethia boulengeri*: Smyth 1974), and polychaeta annelids (*Capitella* sp.: Hill et al.

1988) experienced a significant—in some cases total—loss in fecundity associated with regeneration. This reduction can be manifested through the total number of eggs, the size/mass of individual eggs, the total mass of the brood, and/or egg production and hatching times.

Although all decreases in fecundity directly reduce fitness, allocation trade-offs between regeneration and reproduction may differ between relatively long-lived and relatively short-lived species (Maiorana 1977; Dial and Fitzpatrick 1981; Hill et al. 1988; Smith and Hines 1991b). In long-lived species, total lifetime fecundity is often determined through several breeding seasons. Given a long adult life span with multiple breeding events, the cumulative cost of remaining without a lost appendage (e.g., autotomy) may outweigh the one-time cost of regenerating an appendage; even though this regrowth reduces fecundity in the first breeding season, animals may be able to replenish the lost resources and recover full fecundity before the subsequent breeding events. Regeneration experiments in the long-lived California slender lizard (*B. attenuatus*), for example, found that animals preferentially allocated energy/resources to regeneration at the expense of reproduction (Maiorana 1977).

In contrast, the lifetime fecundity of short-lived species tends to be determined through only a single breeding season. In these species, animals allocate all available resources to reproduction (instead of regeneration) presumably because allocation to appendage regrowth is not cost-effective (i.e., the benefit of regeneration to improve future survivorship does not outweigh the cost of regeneration on lifetime fecundity). Regeneration experiments in the short-lived side-blotched lizard (*U. stansburiana*) and the Texas banded gecko (*C. brevis*) found that animals preferentially allocated resources toward reproduction instead of regeneration (Dial and Fitzpatrick 1981; Fox and McCoy 2000).

It is worth noting that a number of studies failed to detect costs that were predicted to arise from appendage regeneration (survivorship of *P. algerus* or *U. stansburiana*: Althoff and Thompson 1994; Salvador et al. 1995; Niewiarowski et al. 1997; feeding rates of rock lizards *L. monticola*: Martin and Salvador 1993a; growth in blue king crabs *Paralithodes platypus*: Lysenko et al. 2000; growth in common starfish *A. rubens*: Ramsay et al. 2001; growth in hermit crabs *Pagurus longicarpus* or mole crabs *Emerita talpoida*: Weis 1982). However, with some exceptions (Ballinger and Tinkle 1979; Lawrence et al. 1986; Althoff and Thompson 1994; Pomory and Lawrence 1999), many of these experiments were performed in the laboratory and under ad libitum food treatments. Costs associated with the regeneration process might have been offset or alleviated by increased food uptake under these artificial conditions. That is, it is possible in ad libitum conditions that the animal can acquire adequate resources to alleviate trade-offs between regeneration and somatic/reproductive growth. In natural conditions, especially if a lost limb impairs behavior or foraging ability, ad libitum conditions are highly unlikely (Skinner 1985; Vitt and Cooper 1986). Ballinger and Tinkle (1979), for example, compared the effects of regeneration on body growth in the laboratory and in the field; in the laboratory under ad libitum conditions, there was no effect, whereas in the field, regeneration did affect body growth. Similarly, laboratory experiments of Pomory and Lawrence (1999) showed high trade-offs between reproductive and somatic growth in an echinoderm (*Ophiocoma echinata*) only under low food levels.

In summary, regeneration, like autotomy, is associated with numerous and diverse costs. In some cases, these costs can be severe, as in the California slender lizard (*B. attenuatus*), which loses all fecundity as a consequence of tail regeneration (Maiorana 1977). In other cases, these costs may be relatively minor or absent. Regardless, it is clear that in many species both

autotomy and regeneration can be accompanied by important performance or fitness consequences. These consequences can be manifested through many aspects of development, physiology, and behavior and can have important roles in population dynamics/biology (Harris 1989). Multiple individuals experiencing costs associated with the regeneration process, especially those tightly coupled with some aspect of fitness, could have large effects on the whole community (Juanes and Smith 1985). Studies thus far that have incorporated costs associated with the regeneration process into population dynamics and ecology provide an essential background to explore the evolution of regenerative capacities in animals.

REGENERATION AND EVOLUTION

Since the early 1960s, scientists have been interested in the evolution of regeneration, the variation in regenerative tendencies, and how trade-offs associated with autotomy/regeneration might be shaping its presence and/or absence in the animal kingdom (evolution of regeneration: Needham 1961; Spillsbury 1961; Barr 1964; Juanes and Smith 1985; Goss 1987; Vollrath 1990; Wagner and Misof 1992; Carnevali and Bonasoro 2001; evolution of autotomy: Wake and Dresner 1967; Cooper and Vitt 1991; Norman and Finn 2001). As I suggest in the next section, alternative approaches may provide new insights into these questions.

Evolutionary comparisons

Traditionally, studies examining the costs and benefits associated with regeneration compare individuals experiencing autotomy and regeneration with individuals not experiencing autotomy or regeneration (see Regeneration: Performance Costs and Regeneration: Allocation costs). These comparisons are very useful for addressing certain relevant questions to evolutionary biology. For example, comparing the fitness between individuals that have and individuals that have not regenerated is a powerful tool for studying trade-offs associated with the allocation of resources to trait growth; individuals regrowing a lost leg or tail produce a major morphological structure twice, and these individuals can be compared with individuals not regenerating (e.g., producing the structure only one time) to quantify the costs associated with appendage growth. In addition, these studies are the foundation on which I have been able to compile this review. However, to thoroughly explore why regenerative capacities evolve and/or persist (e.g., the evolutionary significance of regeneration), it would be useful to compare individuals who autotomized and regenerated with individuals who autotomized and did not regenerate. The value of making comparisons in this form can best be made explicit by paralleling it to the history of studying alternate mating strategies.

Over the past 20 years, scientists have shifted the way they ask and answer questions regarding the evolutionary significance of an animal's alternative mating tactics (see reviews by Austad 1984; Dominey 1984). Initially, scientists attempted to understand the evolution of alternate mating strategies by comparing the relative fitness of a "major" male (e.g., a male who fights for reproductive success) with that of a "minor" male (e.g., a male who sneaks matings). Two things were subsequently recognized. First, it was determined that, in most cases, whether an individual became a major or minor male depended on unpredictable aspects of the environment and not on the inheritance of specific alleles. For example, whether male dung beetles become a major or minor depends on their larval environment; a male that develops with ample resources will mature into a major, whereas a male that develops with relatively little resources will mature into a minor

(Emlen 2000). Second, it became clear that the mating strategies of these males were based on rules of behavior that specified how best to achieve reproductive success within each of these discrete situations. That is, if a male is in a “good” situation, such as being relatively large, he will adopt a dominant tactic; in a “bad” situation, such as being relatively small, he will adopt a sneaking tactic.

On explicit recognition of these 2 underlying determinants of how and why males adopt a major or minor tactic, new questions arose to better address the evolution of alternate mating tactics. Most important of these was if a male encounters a bad situation, how should it behave? Specifically, do males in this bad situation achieve higher fitness if they perform the major/dominant behavioral tactic or if they switch to an alternate mating tactic? To accurately answer these questions in the light of evolution, researchers began to compare the relative fitnesses of animals in a bad situation that guard with those of animals in that same bad situation that sneak. Once this subtle shift in perspective had been recognized and implemented, the field literally exploded with informative empirical and theoretical research. We now understand many of the selective situations that have shaped the evolution of alternative mating tactics through comparisons between 2 males in bad situations, each employing its own discrete tactic.

This same logic can be applied to studies of the evolutionary significance of appendage regeneration. Individuals regenerating lost appendages are presumably making the best of a bad situation, having had to shed an appendage to survive a predation or a fouled molting event. Similar to alternate mating tactics, unpredictable environmental conditions determine whether or not individuals lose an appendage and end up in a bad situation. Comparing the relative performance/fitness of individuals in this unfortunate situation with that of individuals in a very different situation (e.g., those that have not lost an appendage) is just as indirect as comparing the fitnesses of major males that guard with those of minor males that sneak. To specifically address the evolutionary significance of regeneration, we can ask the following question: given that an individual has lost an appendage, would that individual achieve a higher fitness, on average, if it allocated resources toward regeneration? Or would it do better if it did not expend resources to appendage regrowth and instead remained without the appendage? Consequently, effective exploration of the evolutionary significance of regenerative capacities requires a comparison between animals that autotomize and regenerate and animals that autotomize and do not regenerate (see Figure 1).

Studies making comparisons in this form would perhaps provide more insights as to if, and how, the costs of regeneration may have shaped its presence and/or absence in the animal kingdom. However, such studies are, to my knowledge, absent. One reason for this is that the biologically relevant variation appears to be rare in natural populations: species that autotomize tend to be fixed for their tendency to regenerate. The presumption here is that regeneration is always adaptive, and therefore, why it is fixed in the population. However, the fact that many species are fixed on their ability to (or not to) regenerate merely highlights the need for careful choice of focal species and for novel (e.g., perturbation) experimental approaches in future work.

FUTURE DIRECTIONS

In this final section, I propose research ideas that capitalize on the requisite fitness comparison that allows for explicit consideration of how the costs and benefits of appendage regeneration may be shaping its evolution. They all involve empirical

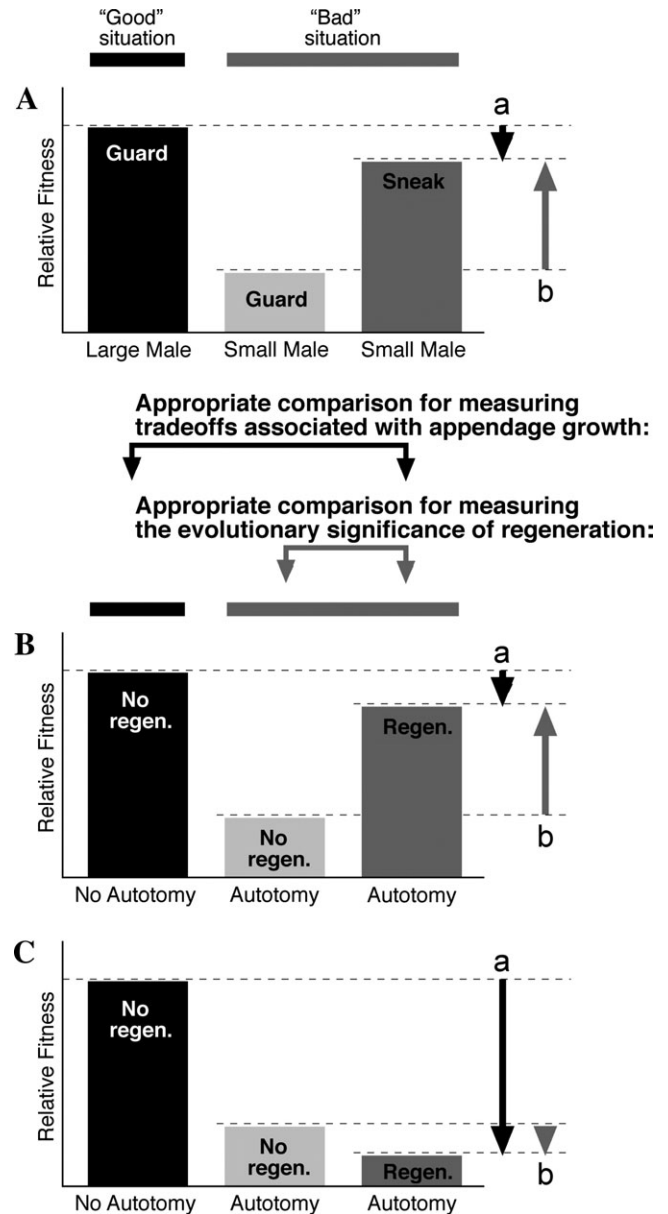


Figure 1

Regeneration research compared with alternate mating tactics. Evolutionary perspectives on the trade-offs associated with regeneration can be paralleled to the trade-offs associated with alternate mating tactics. The benefit of switching to an alternate mating tactic from an evolutionary perspective is made clear through the comparison between 2 males in a bad situation: a small, sneaking male has a higher relative fitness than a small, guarding male (a difference of “b” in panel A). For regeneration, the comparison between an animal in a good situation (no autotomy and no regeneration) and a bad situation (autotomy and regeneration) yields a difference in relative fitness of “a”—the perceived “cost” of regeneration in current literature. An alternative, and perhaps more informative, comparison is between 2 animals in bad situations, both autotomizing but only one regenerating, which yields a difference in relative fitness of b. This relative difference in fitness can be positive (see b in panel B), indicating a net benefit of regeneration, or it can be negative (see b in panel C), indicating a net, or “true,” cost of regeneration.

methods that generate the requisite variation among individuals within a species or that capitalize on such variations as it occurs among species.

First, we could carefully manipulate the timing of autotomy and take advantage of the fact that regeneration takes time. In a captive setting, it is possible to rear 2 groups of individuals: one group that experienced autotomy early in their development and completed the regeneration process and another group that only recently autotomized and did not have time to allocate resources into regeneration. The performance of relevant behaviors of the recently autotomized individuals could then be compared with that of the same-age individuals that already completed the regeneration process. This is perhaps most feasible in species that naturally shed appendages with minimal provocation (e.g., lizards) and could prove most insightful for our understanding of the costs and benefits of regeneration as they relate to locomotion, foraging, and behaviors associated with reproduction. That is, this method would be most useful for behavior or physiology measures that can be measured over a brief period, instead of fitness measures such as fecundity and survivorship that are often determined through lifetime success.

Second, it is possible to engineer the missing phenotype. Again, many species with the ability to regenerate generally do so all the time. Instead of allowing regeneration early in development, we could prevent the regeneration process to create the relevant comparison. Simple cauterizing techniques or perhaps new hormonal/genetic techniques could be applied to species that always regenerate after autotomy and hence prevent the regeneration process. This technique would be especially feasible in species that autotomize at a preformed breakage plane and/or where the rate of regeneration is relatively fast and would permit comparisons between individuals that experience autotomy and regeneration and those prevented from regenerating. In addition, it would allow for comparisons at a range of different developmental stages. That is, we could explore whether the costs of regeneration (compared with the costs of just autotomy) differ based on age and/or maturity; juveniles, nonbreeding adults, and breeding adults might experience different costs from the same developmental phenomenon.

Finally, we could approach the problem from a phylogenetic perspective. Many groups of lizards and spiders, for example, have clades within which there are some species that only autotomize and others that autotomize and then regenerate (e.g., *Agama* lizards: Arnold 1984). We can use the manipulation experiments described above to compare the relative costs and benefits of the 2 types of individuals and then look at whether the costs outweigh the benefits (or vice versa) in the predicted direction. In addition, we could look for correlations between gains and losses of the tendency to regenerate within specific ecological or social/behavioral conditions and try to identify consistent circumstances that are associated with the tendency to (or not to) regenerate. Several species of spiders, for example (*Leiobunum nigripes*, *H. pluchei*), are capable of autotomy but not regeneration. Missing appendages in these species has no apparent performance cost in situations relating to foraging, mating, and/or survivorship (Guffey 1998; Johnson and Jakob 1999; Dodson and Schwaab 2001). Although this scenario makes evolutionary sense (e.g., if there is no performance cost to missing the appendage, then selection should not favor the potentially costly allocation of resources to regenerate it), we currently do not have research to support this idea. Both testing the predictions about trade-offs and looking for correlations within clades (such as lizards or spiders) could offer further insights into the selective pressures on the tendency to regenerate after autotomy.

Perhaps the best approach to this problem will involve further exploration into those species that are naturally variable in their tendency to regenerate. Some crustaceans, for

example (see Altered Development), will only regenerate lost limbs outside of the breeding season or at certain developmental stages. Some insects show the same pattern; mantids (Karuppanan 1998) and true bugs (Lüscher 1948), for example, are only capable of regenerating limbs if they are lost early in development. Similar to the approaches described above, careful manipulation of the timing of autotomy and regeneration would allow for natural comparisons of individuals experiencing autotomy without regeneration with those experiencing autotomy with regeneration. Although all known facultative cases I found exist in arthropods, researchers may have not specifically looked for this variation in other taxa, and it is possible that it occurs in vertebrates as well.

It will be critical for modern researchers to look for variation in the expression of regeneration. Although it is clear that a breadth of taxa regularly shed and regrow body parts (see Table 1 and Appendix), it will be the subset of species that vary in their regenerative tendencies that are likely to be the most promising for empirical studies of the evolution of regeneration. A combination of phenotype engineering, laboratory experiments, phylogenetic comparisons, and further sampling of natural populations provides ideal opportunities for researchers to be explicit about the costs and benefits of autotomy and, perhaps more importantly, the costs and benefits of regeneration.

Exploring when and where regenerative tendencies have evolved, and why, promises to bring studies of this phenomenon full circle. Exciting advances await researchers able to explore the evolution of regeneration in its natural context. It is likely that a myriad of factors influence the trade-offs, and hence the selective pressures, associated with autotomy and regeneration. Some of these potential factors include foraging methods, locomotion, habitat type, predator and prey densities, appendage function, extent of autotomy, pattern and speed of regeneration, phylogeny, general life-history traits, and the condition (health/age/sex) of the animal. Including these factors into comparisons on an evolutionary level will allow us to specifically look at how regeneration, one of the most primitive developmental processes, has shaped the animal form and function. Asking evolutionary questions will be essential for advancing our understanding of the evolution of regenerative tendencies, and future work will hopefully provide generalizations about what the costs of regeneration are and how they affect fitness.

APPENDIX

Species with regenerative tendencies

Class and species	Ability	Reference
Reptilia		
<i>Acontias</i> spp.	Poor	Arnold (1985)
<i>Agama agama</i>	Fair–good	Arnold (1984)
<i>Agama adramitana</i>	Fair	Arnold (1984)
<i>Agama agrorensis</i>	Good	Arnold (1984)
<i>Agama annectans</i>	Fair	Arnold (1984)
<i>Agama atra</i>	Poor	Arnold (1984)
<i>Agama atricollis</i>	Good	Arnold (1984)

Appendix, continued

Class and species	Ability	Reference			
<i>Agama benueensis</i>	Poor	Arnold (1984)	<i>Eumeces gilberti</i>	Fair	Bellairs and Bryant (1985)
<i>Agama bibronii</i>	Fair	Arnold (1984)	<i>Eumeces laticeps</i>	Good	Vitt and Cooper (1986)
<i>Agama boueti</i>	Fair	Arnold (1984)	<i>Eumeces fasciatus</i>	Fair–good	Bellairs and Bryant (1985)
<i>Agama caudospinosa</i>	Fair	Arnold (1984)	<i>Eumeces skiltonianus</i>	Good	Bellairs and Bryant (1985)
<i>Agama caucasica</i>	Fair	Arnold (1984)	<i>Gekko gekko</i>	*	Rumping and Jayne (1996)
<i>Agama cyanogaster</i>	Good	Arnold (1984)	<i>Gerrhonotus multicarinatus</i>	Fair	Bellairs and Bryant (1985)
<i>Agama doriae</i>	Poor	Arnold (1984)	<i>Hemidactylus brooki</i>	Fair	Magon (1982)
<i>Agama himalayana</i>	Good	Arnold (1984)	<i>Hemidactylus flaviviridis</i>	Fair	Ndukuba (1993)
<i>Agama melanura</i>	Good	Arnold (1984)	<i>Hemidactylus frenatus</i>	Fair	Jayadeep (1993)
<i>Agama nupta</i>	Fair	Arnold (1984)	<i>Hemidactylus garnoti</i>	Fair	Bellairs and Bryant (1985)
<i>Agama paragama</i>	Good	Arnold (1984)	<i>Hemidactylus turcicus</i>	Fair	Bellairs and Bryant (1985)
<i>Agama phillipsii</i>	Good	Arnold (1984)	<i>Hemiergis peronii</i>	Good	Smyth (1974)
<i>Agama planiceps</i>	Fair	Arnold (1984)	<i>Lacerta agilis</i>	Good	Bellairs and Bryant (1985)
<i>Agama rueppelli</i>	Poor	Arnold (1984)	<i>Lacerta dugesii</i>	Good	Bellairs and Bryant (1985)
<i>Agama sankaranika</i>	Poor	Arnold (1984)	<i>Lacerta lepida</i>	Good	Baranowitz et al. (1979)
<i>Agama spinosa</i>	Fair	Arnold (1984)	<i>Lacerta monticola</i>	Good	Martin and Salvador (1993a, 1993b)
<i>Agama stellio</i>	Good	Arnold (1984)	<i>Lacerta vivipara</i>	Good	Oppliger and Clobert (1997)
<i>Agama stoliczkana</i>	Poor	Arnold (1984)	<i>Lampropholis guichenoti</i>	*	Purvis (1979)
<i>Agama sylvanus</i>	Poor	Arnold (1984)	<i>Lygosoma laterale</i>	*	Clark (1969)
<i>Agama tuberculata</i>	Fair	Arnold (1984)	<i>Lophognathus temporalis</i>	Good	Arnold (1984)
<i>Agama yemenensis</i>	Fair	Arnold (1984)	<i>Lygodactylus klugei</i>	Fair	Bellairs and Bryant (1985)
<i>Amblyrhynchus</i> spp.	Poor	Bellairs and Bryant (1985)	<i>Mabuya carinata</i>	*	Radhakrishnan and Shah (1986)
<i>Amphibolurus caudicinctus</i>	Fair	Arnold (1984)	<i>Mabuya heathi</i>	Good	Vitt (1981)
<i>Anguis fragilis</i>	Poor	Bellairs and Bryant (1985)	<i>Melanoseps</i> spp.	Poor	Arnold (1985)
<i>Anniella pulchra</i>	Poor	Bellairs and Bryant (1985)	<i>Melanosuchus niger</i>	Fair	Bellairs and Bryant (1985)
<i>Anolis carolinensis</i>	Fair	Tassava and Goss (1966)	<i>Morethia boulengeri</i>	Good	Smyth (1974)
<i>Batrachoseps attenuatus</i>	Good	Maiorana (1977)	<i>Ophiodes</i> spp.	Poor	Arnold (1985)
<i>Brachylophus</i> spp.	Poor	Bellairs and Bryant (1985)	<i>Ophiomorus parachalcides</i>	Poor	Arnold (1985)
<i>Bumopus tuberculatus</i>	Fair	El-Karim (1994)	<i>Ophiomorus scelotes</i>	Poor	Arnold (1985)
<i>Caiman crocodilus</i>	*	Bellairs and Bryant (1985)	<i>Ophiomorus sphenops</i>	Poor	Arnold (1985)
<i>Calotes cristatellus</i>	Fair	Bellairs and Bryant (1985)	<i>Ophiomorus streeti</i>	Poor	Bellairs and Bryant (1985)
<i>Coleonyx brevis</i>	Good	Dial and Fitzpatrick (1981)	<i>Ophisaurus attenuatus</i>	Poor	Bryant (1985)
<i>Coleonyx variegates</i>	Good	Bellairs and Bryant (1985)	<i>Phyllodactylus marmoratus</i>	Good	Fitch (2003)
<i>Cnemidophorus sexlineatus</i>	Fair	Fitch (2003)	<i>Physignathus lesueurii</i>	Good	Daniels (1984)
<i>Dipsosaurus</i> spp.	Fair–good	Bellairs and Bryant (1985)	<i>Podarcis dugesii</i>	Good	Hardy CJ and Hardy CM (1977)
			<i>Podarcis muralis</i>	Good	Bellairs and Bryant (1985)
			<i>Podarcis sicula</i>	*	Brown et al. (1995)
			<i>Psammmodromus algirus</i>	Good	Bellairs and Bryant (1985)
			<i>Sceloporus jarrovi</i>	Good	Salvador et al. (1995)
			<i>Sceloporus scalaris</i>	Good	Ballinger and Tinkle (1979)
					Ballinger and Tinkle (1979)

Appendix, continued

Class and species	Ability	Reference			
<i>Sceloporus undulatus</i>	Good	Ballinger and Tinkle (1979)	<i>Pleurodeles waltl</i>	*	Arsanto et al. (1992)
<i>Sphaerodactylus argus</i>	Fair-good	Bellairs and Bryant (1985)	<i>Pseudacris clarki</i>	Fair	Scadding (1981)
<i>Sphenomorphus quoyii</i>	Good*	Daniels (1985)	<i>Pseudacris triseriata</i>	Poor-fair	Scadding (1980)
<i>Spaerodactylus goniorhynchus</i>	Fair-good	Hughes and New (1959)	<i>Rana brevipoda porosa</i>	Fair	Kurabuchi and Inoue (1982)
<i>Uta stansburiana</i>	Good	Fox and Rostker (1982)	<i>Rana cyanophlyctis</i>	Poor-fair	Scadding (1980)
<i>Xantusia vigilis</i>	Fair-good	Bellairs and Bryant (1985)	<i>Rana japonica</i>	Fair	Kurabuchi and Inoue (1982)
Amphibia			<i>Rana pipiens</i>	Poor	Pollack and Maheras-Rarick (1990)
<i>Ambystoma jeffersonianum</i>	Good	Scadding (1977)	<i>Rana ridibunda ridibunda</i>	Fair	Scadding (1981)
<i>Ambystoma gracile</i>	*	Nebeker et al. (1994)	<i>Rana rugosa</i>	Fair	Kurabuchi and Inoue (1982)
<i>Ambystoma laterale</i>	Good	Scadding (1977)	<i>Rhacophorus arboreus</i>	Fair	Kurabuchi et al. (1985)
<i>Ambystoma opacum</i>	Good	Scadding (1981)	<i>Rhacophorus buergeri</i>	Fair	Kurabuchi et al. (1985)
<i>Ambystoma maculatum</i>	Fair	Scadding (1980)	<i>Rhacophorus schlegelii</i>	Fair	Kurabuchi et al. (1985)
<i>Ambystoma mexicanum</i>	Good	Scadding (1981)	<i>Salamandra salamandra</i>	Poor-fair	Scadding (1981)
<i>Ambystoma tigrinum</i>	Poor	Scadding (1980)	<i>Siren intermedia</i>	Poor	Scadding (1977)
<i>Amphiuma means</i>	Poor-fair	Scadding (1981)	<i>Taricha torosa</i>	Good	Scadding (1981)
<i>Amphiuma tridactylum</i>	Good	Scadding (1978)	<i>Triturus alpestris</i>	Good	Scadding (1981)
<i>Bombina bombina</i>	Fair	Goode (1967)	<i>Triturus cristatus</i>	Good	Scadding (1981)
<i>Bombina variegata</i>	Fair	Goode (1967)	<i>Triturus helveticus</i>	Good	Scadding (1981)
<i>Bufo andersonii</i>	*	Saxena and Jacob (1997)	<i>Triturus marmoratus</i>	*	Ikegami et al. (2002)
<i>Bufo japonicus formosus</i>	*	Kurabuchi (1990)	<i>Triturus pyrrhogaster</i>	Good	Scadding (1981)
<i>Bufo regularis</i>	*	Michael and Hassona (1982)	<i>Triturus vulgaris</i>	Good	Scadding (1981)
<i>Cynops pyrrhogaster</i>	*	Shimizu-Nishikawa et al. (1999)	<i>Xenopus laevis</i>	Fair	Goode (1967)
<i>Desmognathus fuscus</i>	Good	Scadding (1981)	<i>Xenopus mulleri</i>	Fair	Goode (1967)
<i>Desmognathus ochrophaeus</i>	Good	Scadding (1981)	Osteichthyes		
<i>Discoglossus pictus</i>	Fair	Goode (1967)	<i>Aidablennius sphinx</i>	Poor-fair	Wagner and Misof (1992)
<i>Eurycea bislineata</i>	Good	Scadding (1977)	<i>Anolis spp.</i>	Good	Conant (1970)
<i>Gastrophryne carolinensis</i>	Poor	Scadding (1983)	<i>Blennius tentacularis</i>	Poor-fair	Wagner and Misof (1992)
<i>Hyla arborea japonica</i>	Fair	Kurabuchi and Inoue (1982)	<i>Brachydanio rerio</i>	Good	Mari-Beffa et al. (1999)
<i>Hyla crucifer</i>	Poor	Scadding (1982)	<i>Carassius auratus</i>	Good	Caskey and O'Brien (1948)
<i>Hyla septentrionalis</i>	Poor-fair	Scadding (1981)	<i>Cobitis taenia</i>	Good	Wagner and Misof (1992)
<i>Hymenochirus boettgeri</i>	Fair	Goode (1967)	<i>Coryphoblennius galerita</i>	Poor-fair	Wagner and Misof (1992)
<i>Hyperolius viridiflavus</i>	Fair	Scadding (1981)	<i>Cottus bubalis</i>	Poor	Wagner and Misof (1992)
<i>Notophthalmus viridescens</i>	Good	Scadding (1980)	<i>Cottus gobio</i>	Fair	Wagner and Misof (1992)
<i>Plethodon cinereus</i>	Good	Scadding (1977)	<i>Cyprinus carpio</i>	Good	Wagner and Misof (1992)
<i>Plethodon dorsalis</i>	Good	Scadding (1980)	<i>Esox lucius</i>	Good	Wagner and Misof (1992)
<i>Plethodon glutinosus</i>	Good	Scadding (1977)	<i>Fundulus heteroclitus</i>	Good	Goss and Stagg (1957)
			<i>Gobio albipinnatus</i>	Poor-fair	Wagner and Misof (1992)

Appendix, continued

Class and species	Ability	Reference			
<i>Gobio fluviatilis</i>	Good	Wagner and Misof (1992)	<i>Crangon</i> spp.	*	Needham (1965)
<i>Gobio paganellus</i>	Good	Wagner and Misof (1992)	<i>Cyrtograpsus angulatus</i>	Fair–good	Spivak (1990)
<i>Gobius minutus</i>	Good	Wagner and Misof (1992)	<i>Emerita talpoida</i>	Poor	Weis (1982)
<i>Ictalurus nebulosus</i>	Good	Wagner and Misof (1992)	<i>Eupagurus</i>	*	Needham (1965)
<i>Lipophrys canevae</i>	Poor–fair	Wagner and Misof (1992)	<i>Gammarus pulex</i>	Fair–good	Needham (1953)
<i>Macropodus opercularis</i>	Good	Wagner and Misof (1992)	<i>Gecarcinus lateralis</i>	Good	Bliss (1960)
<i>Menidia notata</i>	Good	Wagner and Misof (1992)	<i>Hemigrapsus oregonensis</i>	Good	Kuris and Mager (1990)
<i>Menticirrus</i> sp.	Good	Wagner and Misof (1992)	<i>Homarus americanus</i>	Fair–good	Emmel (1905)
<i>Motella tricurrata</i>	Good	Wagner and Misof (1992)	<i>Homarus gammarus</i>	*	Herrick (1907)
<i>Misgurnus anquilicaudatus</i>	Good	Wagner and Misof (1992)	<i>Leander serratus</i>	Fair–good	Needham (1953)
<i>Misgurnus fossilis</i>	Good	Wagner and Misof (1992)	<i>Necora puber</i>	Good	Norman and Jones (1991)
<i>Oryzias latipes</i>	Good	Wagner and Misof (1992)	<i>Marinogammarus obtusatus</i>	Fair–good	Needham (1953)
<i>Paralipophrys trigloides</i>	Fair	Wagner and Misof (1992)	<i>Menippe mercenaria</i>	Fair–good	Savage et al. (1975)
<i>Perca fluviatilis</i>	Fair	Wagner and Misof (1992)	<i>Orchestia cavimana</i>	Fair–good	Needham (1953)
<i>Periophthalmus</i> spp.	Good	Wagner and Misof (1992)	<i>Orconectes virilis</i>	*	Mittenthal and Nuelle (1988)
<i>Protopterus annectens</i>	Fair	Conant (1970)	<i>Oziotelphusa senex senex</i>	*	Reddy et al. (1983)
<i>Protopterus aethiopicus</i>	Fair	Conant (1970)	<i>Pachygrapsus crassipes</i>	Good	Hiatt (1948)
<i>Salaria fluviatilis</i>	Poor–fair	Wagner and Misof (1992)	<i>Pachygrapsus</i> spp.	*	Needham (1965)
<i>Salaria incognitos</i>	Poor–fair	Wagner and Misof (1992)	<i>Pagurus longicarpus</i>	Good	Weis (1982)
<i>Salaria pavo</i>	Poor–fair	Wagner and Misof (1992)	<i>Palaemon elegans</i>	*	Webster (1983)
<i>Salaria sanguinolentus</i>	Good	Wagner and Misof (1992)	<i>Palaemon serratus</i>	Good	Bliss (1960)
<i>Salmo fario</i>	Good	Wagner and Misof (1992)	<i>Paralithodes camtschatica</i>	Good	Edwards (1972)
<i>Sphaerodactylus</i> spp.	Fair	Conant (1970)	<i>Paralithodes platypus</i>	Good	Lysenko et al. (2000)
<i>Syngnathus acus</i>	Good	Wagner and Misof (1992)	<i>Penaeus indicus</i>	*	Srinivasulu Reddy and Ramana Rao (1986)
<i>Tilapia melanophleura</i>	Fair–good	Becerra et al. (1996)	<i>Penaeus monodon</i>	*	Srinivasulu Reddy and Ramana Rao (1989)
<i>Tilapia mossambica</i>	Good	Wagner and Misof (1992)	<i>Pilumnus hirtellus</i>	*	Demeusy et al. (1994)
<i>Tinca vulgaris</i>	Good	Wagner and Misof (1992)	<i>Porcellana platycheles</i>	Fair–good	Needham (1953)
<i>Trochogaster</i> spp.	Good	Conant (1970)	<i>Procambarus acutus</i>	Fair	Mittenthal and Nuelle (1988)
<i>Tritogaster</i> spp.	Good	Tassava and Goss (1966)	<i>Procambarus clarkii</i>	Fair	Mittenthal and Nuelle (1988)
<i>Trichogaster sumatrans</i>	Good	Wagner and Misof (1992)	<i>Sesarma haematocheir</i>	*	Suzuki (1985)
Crustacea			<i>Talitrus saltator</i>	Fair–good	Needham (1953)
<i>Acanthonyx lunulatus</i>	*	Laugier and Chaix (1985)	<i>Uca chlorophthalmus</i>	*	Mohrherr (1987)
<i>Alpheus heterochelis</i>	*	Read and Govind (1998)	<i>Uca lacteal</i>	*	Mohrherr (1987)
<i>Asellus aquaticus</i>	Good	Bliss (1960)	<i>Uca pugilator</i>	Good	Hopkins (1993)
<i>Callinectes sapidus</i>	Fair–good	Smith (1992)	Echinodermata		
<i>Cambarus propinquus</i>	Good	Zeleny (1905)	<i>Acanthaster planci</i>	*	Lawrence (1991)
<i>Cambarus</i> spp.	*	Needham (1965)	<i>Acrochida brachiata</i>	Fair–good	Sköld and Rosenburg (1996)
<i>Carcinus maenas</i>	Fair–good	Needham (1953)	<i>Allostichaster insignis</i>	*	Lawrence (1991)
<i>Chionoecetes bairdi</i>	Good	Edwards (1972)			
<i>Chionoecetes opilio</i>	*	Miller and Watson (1976)			

Appendix, continued

Class and species	Ability	Reference		Ability	Reference
<i>Amphipholis squamata</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Ophiuroglypha lymani</i>	Fair-good	Sköld and Rosenburg (1996)
<i>Amphiura chiajei</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Paracentrotus lividus</i>	Good	Dubois and Ameye (2001)
<i>Amphiura filiformis</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Patiria chilensis</i>	*	Lawrence (1991)
<i>Archaster typicus</i>	*	Lawrence (1991)	<i>Patiriella pseudoexigua</i>	*	Lawrence (1991)
<i>Asterias forbesi</i>	*	Lawrence (1991)	<i>Pisaster giganteus</i>	*	Lawrence (1991)
<i>Asterias rubens</i>	Good	Dubois and Ameye (2001)	<i>Pisaster ochraceus</i>	*	Lawrence (1991)
<i>Asterias vulgaris</i>	*	Lawrence (1991)	<i>Pycnopodia helianthoides</i>	*	Lawrence (1991)
<i>Astropecten americanus</i>	*	Lawrence (1991)	<i>Sclerasterias mollis</i>	*	Lawrence (1991)
<i>Astropecten articulatus</i>	*	Lawrence (1991)	<i>Solaster dawsoni</i>	*	Lawrence (1991)
<i>Astrostole scabra</i>	*	Lawrence (1991)	<i>Solaster stimpsoni</i>	*	Lawrence (1991)
<i>Coscinasterias calamaria</i>	*	Lawrence (1991)	<i>Stichaster striatus</i>	*	Lawrence (1991)
<i>Evasterias troscheli</i>	*	Lawrence (1991)	<i>Strongylocentrotus purpuratus</i>	Good	Dubois and Ameye (2001)
<i>Heliaster helianthoides</i>	*	Lawrence (1991)	Insecta		
<i>Leptasterias aequalis</i>	*	Lawrence (1991)	<i>Anisolabis</i> spp.	Fair	Bulliere D and Bulliere F (1985)
<i>Leptasterias hexactis</i>	*	Lawrence (1991)	<i>Asellus</i> spp.	Fair	Needham (1965)
<i>Leptasterias tenera</i>	*	Lawrence (1991)	<i>Baculum</i> spp.	Good	Carlberg (1986)
<i>Linchia</i> spp.	Good	Carnevali (2001)	<i>Blabera craniifer</i>	Fair	Bulliere (1970)
<i>Luidia clathrata</i>	*	Lawrence (1991)	<i>Blaberus</i> spp.	Fair	Bulliere D and Bulliere F (1985)
<i>Luidia magellanica</i>	*	Lawrence (1991)	<i>Blatella</i> spp.	Fair	Brindley (1897)
<i>Marthasterias glacialis</i>	*	Lawrence (1991)	<i>Blatella</i> spp.	Fair	Bulliere D and Bulliere F (1985)
<i>Meyenaster gelinosus</i>	*	Lawrence (1991)	<i>Blattela germanica</i>	Fair	Woodfruff (1937)
<i>Ophiactis asperula</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Blattidae</i> spp.	Fair	Bulliere D and Bulliere F (1985)
<i>Ophioderma longicaudum</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Bombyx</i> spp.	Poor	Bulliere D and Bulliere F (1985)
<i>Ophioglypha</i> spp.	Good	Zeleny (1905)	<i>Cambarus</i> spp.	Fair	Needham (1965)
<i>Ophioscolex nutrix</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Carausius morosus</i>	Good	TL Maginnis (in preparation)
<i>Ophiothrix fragilis</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Chloeon</i> spp.	Fair	Needham (1965)
<i>Ophiothrix nigra</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Culex</i> spp.	Poor	Bulliere D and Bulliere F (1985)
<i>Ophiothrix quinquemaculata</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Dixippus</i> spp.	Good	Needham (1965)
<i>Ophiura albida</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Enallagma boreale</i>	Fair	Parvin and Cook (1968)
<i>Ophiura ophiura</i>	Fair-good	Sköld and Rosenburg (1996)	<i>Ephestia</i> spp.	Poor	Bulliere D and Bulliere F (1985)
			<i>Ephippiger ephippiger</i>	Fair	Lakes and Mücke (1989)
			<i>Euantissa pulchra</i>	Fair	Karuppanan (1998)
			<i>Eupagurus</i> spp.	Fair	Needham (1965)

Appendix, continued

Class and species	Ability	Reference			
<i>Gryllus</i> spp.	Fair	Bulliere D and Bulliere F (1985)	<i>Anyphaena accentuata</i>	*	Vollrath (1990)
<i>Gromphadorhina</i> spp.	Fair	Bulliere D and Bulliere F (1985)	<i>Araneus diadematus</i>	*	Vollrath (1990)
<i>Ischnura cervula</i>	Fair	Parvin and Cook (1968)	<i>Argas persicus</i>	Fair	Nuttall (1920)
<i>Ischnura perparva</i>	Fair	Parvin and Cook (1968)	<i>Argyroneta aquatica</i>	*	Vollrath (1990)
<i>Lepisma</i> spp.	Good	Bulliere D and Bulliere F (1985)	<i>Coelotes terrestris</i>	*	Vollrath (1990)
<i>Leptinotarsa</i> spp.	Poor	Bulliere D and Bulliere F (1985)	<i>Cupiennius salei</i>	*	Vollrath (1990)
<i>Leucophaea maderae</i>	Good	Shaw and Bryant (1974)	<i>Dolomedes fimbriatus</i>	*	Vollrath (1990)
<i>Leucophaea</i> spp.	Fair	Bulliere D and Bulliere F (1985)	<i>Dugesia hentzi</i>	*	Vollrath (1990)
<i>Oncopeltus fasciatus</i>	Fair	Wolsky (1957)	<i>Dugesia californica</i>	*	Vollrath (1990)
<i>Pachygrapsus</i> spp.	Fair	Needham (1965)	<i>Heteropoda venatoria</i>	*	Vollrath (1990)
<i>Periplaneta americana</i>	Fair	Kubo et al. (1991)	<i>Heterophrynus elaphus</i>	*	Igelmund (1987)
Phasmatodea (order)	Good	Brock (1999) and TL Maginnis (personal observation)	<i>Hyalomma aegyptium</i>	Fair	Nuttall (1920)
<i>Platycnemis</i> spp.	Fair	Bulliere D and Bulliere F (1985)	<i>Ixodes ricinus</i>	Fair	Nuttall (1920)
<i>Rhodnius prolixus</i>	Fair	Lüscher (1948)	<i>Latrodectus mactans</i>	Poor	Vollrath (1990)
<i>Rhodnius</i> spp.	Fair	Needham (1965)	<i>Lycosa</i> spp.	*	Vollrath (1990)
<i>Sipylloidea sipylus</i>	Good	Maginnis (2006)	<i>Lycosa singoriensis</i>	*	Vollrath (1990)
<i>Sphodromantis</i>	Fair	Needham (1965)	<i>Metaphidippus aeneolus</i>	*	Vollrath (1990)
<i>Teleogryllus commodus</i>	Fair	Bulliere D and Bulliere F (1985)	<i>Metellina nerianae</i>	*	Vollrath (1990)
<i>Telea</i> spp.	Poor	Bulliere D and Bulliere F (1985)	<i>Microlinyphia impigra</i>	*	Vollrath (1990)
<i>Tenebrio</i> spp.	Poor	Bulliere D and Bulliere F (1985)	<i>Misumena vatia</i>	*	Vollrath (1990)
<i>Timarchia</i> spp.	Poor	Bulliere D and Bulliere F (1985)	<i>Nuctenea umbratica</i>	*	Vollrath (1990)
<i>Troglophilus</i> spp.	Fair	Bulliere D and Bulliere F (1985)	<i>Olios fasciculatus</i>	*	Vollrath (1990)
<i>Vanessa</i> spp.	Poor	Bulliere D and Bulliere F (1985)	<i>Pirata piraticus</i>	*	Vollrath (1990)
Arachnida			<i>Salticus</i> spp.	*	Vollrath (1990)
<i>Agelena labryinthica</i>	*	Vollrath (1990)	<i>Schizocosa ocreata</i>	Fair	Uetz et al. (1996)
<i>Amaurobius fenestralis</i>	*	Vollrath (1990)	<i>Segestria florentina</i>	*	Vollrath (1990)
<i>Amaurobius similis</i>	*	Vollrath (1990)	<i>Segestria senoculata</i>	*	Vollrath (1990)
<i>Amblyoma herbraeum</i>	Fair	Nuttall (1920)	<i>Tegenaria domestica</i>	*	Vollrath (1990)
			<i>Tegenaria atrica</i>	*	Vollrath (1990)
			<i>Tetragnatha extensa</i>	*	Vollrath (1990)
			<i>Textrix denticulate</i>	*	Vollrath (1990)
			<i>Thomisus onustus</i>	*	Vollrath (1990)
			<i>Tibellus oblongus</i>	*	Vollrath (1990)
			<i>Trochosa</i> spp.	*	Vollrath (1990)
			Miscellaneous		
			<i>Asellus aquaticus</i>	*	Needham (1953)
			<i>Marinogammarus obtusatus</i>	*	Needham (1953)
					Isopod
					Scud

Appendix, continued

Class and species	Ability	Reference	
<i>Muraenesox talabonoides</i>	Fair	George (1978)	Eel
<i>Octopus aranea</i>	Fair	Norman and Finn (2001)	Octopod
<i>Octopus horridus</i>	Fair	Norman and Finn (2001)	Octopod
<i>Octopus mutilans</i>	Fair	Norman and Finn (2001)	Octopod
<i>Octopus tonganus</i>	Fair	Norman and Finn (2001)	Octopod
<i>Phidiana crassicornis</i>	*	Miller and Byrne (2000)	Nudibranch
Polychaeta species	Fair	Hill et al. (1988)	Annelid
<i>Prophysaon andersoni</i>	Fair	Hand and Ingram (1950)	Gastropod
<i>Prophysaon foliolatum</i>	Fair	Hand and Ingram (1950)	Gastropod

Good = a complete or near-complete regenerated appendage is eventually formed. Adults may or may not be capable of regeneration, but immature individuals are. Fair = a partial appendage regrows during development. Poor = a weak appendage regrows; it does not come close to obtaining full proportions. Asterick = based on the literature, appendage regeneration in these species is certain, but I was unable to ascertain the quality of the regenerated appendage.

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