

Genitalic Traits of Mammals

Systematics and Variation

EDWARD H. MILLER

INTRODUCTION

Most early anatomists did not believe in evolution (Coleman 1964; Sloan 1992), but nevertheless used reproductive traits in classification. The renowned anatomist Richard Owen did not believe in Darwinian natural selection, for example, but made recommendations about classification on anatomical grounds, such as proposing that *Homo* be elevated to the rank of subclass (“Archencephala”) within Mammalia. Early anatomical information about reproductive traits helped to establish higher-level mammalian classification. For example, on the basis of female reproductive anatomy, the great French systematist Henri de Blainville distinguished monotremes and marsupials from placental mammals in 1816, and then further separated monotremes from marsupials in 1834 (Huxley 1864; Simpson 1945). Resulting classifications were in the tradition of hierarchical nested classifications of the day, and superficially resembled phylogenetically based schemes that are so familiar today. However, those classifications were similarity-based and without formal reference to ancestor–descendant relationships; today, formal

phylogenetic analyses permeate all aspects of comparative studies.

Adaptive interpretations of reproductive morphology also have changed. Interspecific differences in genitalic structure were long interpreted as adaptive mechanical isolating mechanisms to reduce hybridization (Mayr 1963; Dobzhansky 1970). However, interspecific diversity could not be satisfactorily explained within such paradigms, as expressed by the primate biologist and anatomist W. C. O. Hill: “It is remarkable, considering that the organs have the same rather limited functions to perform, how varied the male genitalia of primates are in their morphology” (quoted by Dixson 1998, p. 244). At present, genitalic diversity is viewed primarily as an evolutionary consequence of sexual selection¹ by mate choice (Eberhard 2004a, b, 2006; Hosken & Stockley 2004). Early literature on genitalic diversity and sexual selection was strongly biased toward males, partly because female traits simply were viewed as less interesting (“more common than elaborate, more utilitarian than bizarre”; Gowaty 1997, p. 353). This bias resulted in little attention being paid to female sexual traits

1. The artificiality of this concept is increasingly recognized. West-Eberhard (1983) included it within a more broadly conceived notion of social selection. Paterson (1993) pointed out that traits ascribed to sexual selection are used for multiple social purposes, and de Waal (1988, p. 232), in referring to bonobo (*Pan paniscus*) behavior, used the term sociosexual, because much of that species’ so-called sexual behavior “is divorced from reproductive functions”.

or to the roles of inter-sexual interactions in shaping genitalic evolution. This is no longer the case (Eberhard 1996; Arnqvist & Rowe 2005).

High interspecific variation characterizes sexually-selected systems as disparate as birdsong, primate sexual skin, and phallic morphology (Eberhard 1985; Stallmann & Froelich 2000; figure 21.1). Variation attributable to sexual selection also occurs intraspecifically (geographically, and within local populations). In this chapter I will explore the theme of variation (mainly genitalic) with reference to systematics, inter- and intraspecific patterns, and derived uses of genitalia in communication. The relative dearth of information on females unfortunately means that this chapter continues the tradition of male bias.

THE USE OF REPRODUCTIVE MORPHOLOGY IN PHYLOGENETIC INFERENCE

Like all traits, reproductive structures express both diversity and conservatism. The male reproductive system comprises penis, testes, epididymides, deferent ducts, and accessory glands, but these vary in form and function across major clades (Setchell &

Breed 2006). A penis is present and delivers semen in all mammals, but penile anatomy varies greatly. The penis of marsupials and placental mammals transmits urine and sexual products, but in monotremes the urine passes to a collecting chamber for elimination via the cloaca, and the penis functions only to transmit sexual products.

Accessory reproductive glands of males also illustrate high-level variation. The main types are prostate gland, vesicular gland (= seminal vesicles), bulbourethral gland (= Cowper's gland), and ampullary gland; mucous glands (the Littre glands) and modified sebaceous glands (the preputial glands) also occur in some species (Voss 1979; Setchell & Breed 2006). The main kinds of glands are present in many species, but size, morphology, and even presence-absence vary greatly. For example, all four of the main types of glands are present in most rodents (figure 21.2A), but only prostate and bulbourethral glands occur in the blind mole rat (*Spalax ehrenbergi*; Gottreich et al. 2001). In the Carnivora, only the prostate is uniformly present, the ampullary gland is variably present (e.g., it occurs in dogs, *Canis familiaris*), and vesicular and bulbourethral glands are always absent (figure 21.2A); only the prostate is present in Cetacea (Rommel et al. 2007).

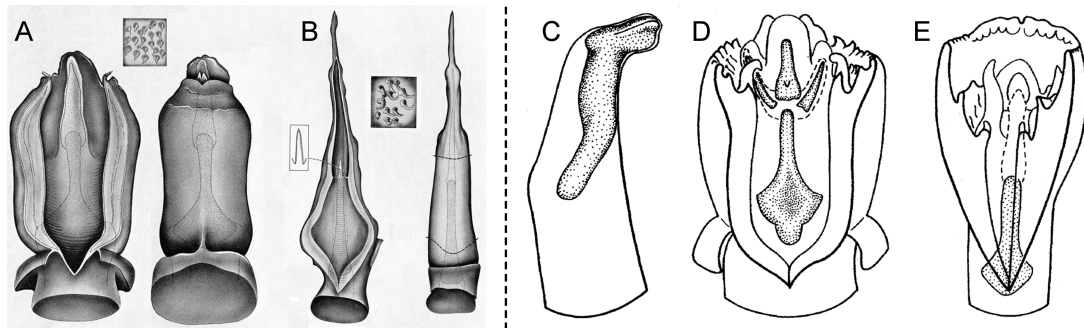


FIGURE 21.1 Sexually-selected structures typically vary greatly, even among related species. Phallic anatomy of rodents exemplifies this trend. Left of dashed line: Glans penis of white-throated woodrat (*Neotoma albigula*; A) and bushy-tailed woodrat (*N. cinerea*; B). For each species, the glans is shown (left) incised mid-ventrally to expose lumen of urethra, crater, and baculum (os penis), and (right) in ventral aspect; the insets are enlargements that show the spines which cover most of the surface of the glans. Both the bacular bone and cartilaginous apex are shown. Right of dashed line: Bacular size, morphology, and proximity to the penile surface vary across species, and influence exposure of this bone to direct selection during intromission. C, Superficial bacular position in Uinta chipmunk (*Tamias umbrinus*; left lateral view). D, Intermediate bacular position in southern red-backed vole (*Clethrionomys gapperi*; mid-ventral incised view, showing bacular shaft plus three apical processes). E, Deeply embedded bacular position in chestnut pogonomys (*Pogonomys macrourus*; incised mid-ventral view). A and B after Hooper (1960: plates I and VII); C–E after Patterson (1983: figure 1).

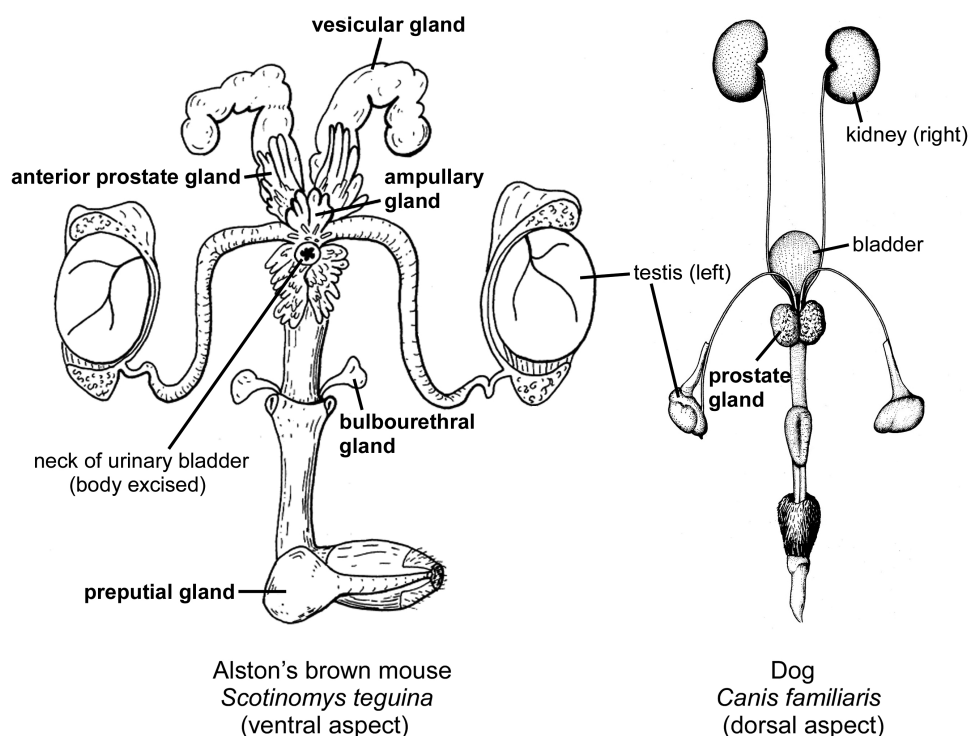


FIGURE 21.2 Diverse reproductive accessory glands occur in male mammals, but vary greatly in morphology and presence/absence in different species. All main types are present in most rodents (A, Alston's brown mouse *Scotinomys teguina*), but only one or two kinds are present in the Carnivora (prostate and ampullary glands are present in the dog *Canis familiaris*; B). (A), after Carleton et al. (1975: figure 2); (B), after Raynaud (1969: figure 441).

These joint patterns of diversity and conservatism give reproductive attributes value as high-level taxonomic traits, and these point to some clear patterns. The epididymis is present in all mammals; other structures (e.g., bulbourethral glands) presumably were present in the common ancestor to mammals, as they occur in extant monotremes, marsupials, and most placental mammals (Setchell & Breed 2006).² However, reliance on morphological traits also has caused considerable taxonomic instability. An example is the traditional Order Insectivora. Simpson (1945, pp. 48–53, 176; see Symonds 2005) placed varied insectivorous placental mammals in this taxon: tenrecs, elephant-shrews, tree shrews, and moles. Simpson (1945, p. 175; Symonds 2005) noted that characters of Insectivora

were “in great part primitive for all placental mammals”. Candidates are sperm crypts in the oviduct, which are present in moles but absent in hedgehogs, tenrecs, and golden moles (Bedford et al. 2004); and a shallow cloaca, which is present in tenrecs and some shrews (Symonds 2005). In addition, all Insectivora except tree shrews have inguinal testes (Findley 1968). The artificial nature of the Order Insectivora has been revealed by molecular studies, which distribute its members across several clades (figure 21.3). Morphological traits now serve a subsidiary role in phylogenetic analysis, and are more valuable for elucidating patterns and rates of evolutionary change, rather than as a source of information for phylogenetic inference (Springer et al. 2007). For example, molecular data enable

2. Clear homology statements are needed in such discussions (Hall 1994). For example, the penis is homologous as an intromittent organ in all male mammals; but is homologous as a dual-function organ (for intromission and urination) only in marsupials and placental mammals.

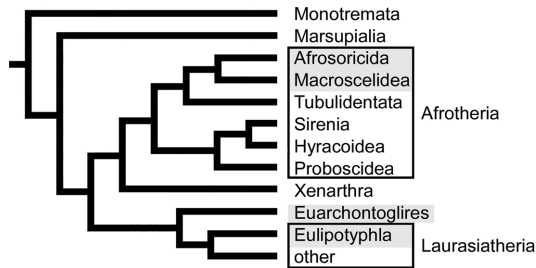


FIGURE 21.3 Terrestrial insectivores (tenrecs, golden moles, hedgehogs, shrews, etc.), and sometimes also elephant shrews (Macroscelidea) and tree shrews (Scandentia), were traditionally placed together in the Insectivora (= Lipotyphla). This is now known to be an unnatural grouping, because it included: two sister groups within the Afrotheria (Afrosoricida, Macroscelidea); several families within Laurasiatheria (solenodons, shrews, etc.); and Scandentia within the Euarchontoglires. Groups that have been included in Lipotyphla are marked by gray. After Murphy et al. (2007: figure 6) and Springer and Murphy (2007b: p. 699).

the estimation of when structures like bulbourethral glands arose: they must date to ≥ 215 Ma, when monotremes last shared a common ancestor with other mammals (Springer & Murphy 2007a, b). A synapomorphy of Afrotheria (tenrecs, golden moles, elephant shrews, sirenians, elephants, aardvarks, and hyraxes) is the trait of being primary testicond mammals, with testes remaining close to the kidney within the body cavity (Gaeth et al. 1999; Bedford et al. 2004; Setchell & Breed 2006; Seiffert 2007); this condition must be ancient, as Afrotheria and Xenarthra diverged from one another ~ 100 Ma (Springer & Murphy 2007a, b). Another example is the independent loss of bulbourethral glands in Cetacea and Carnivora, which can be dated minimally to the origins of those clades at ~ 80 and ~ 50 Ma, respectively (Murphy et al. 2007; Springer & Murphy 2007a, b). A final example is position of the testes in Pinnipedia. Some non-reproductive morphological data support a sister-group relationship between walruses (Odobenidae: *Odobenus rosmarus*) and seals (Phocidae; Wyss & Flynn 1992; Berta & Wyss 1994). Testes position is phylogenetically ambiguous: in phocids, testes are close to the ventral abdominal wall, whereas they are scrotal (pendulously scrotal in the rut) in fur seals and sea lions (Otariidae; Scheffer 1950; Stewardson et al. 1998). Testes in the walrus are

intermediate, as they “are situated outside the muscular abdominal wall, in the blubber lateral to the base of the penis, more as in the Phocidae as in the Otariidae” (Fay 1982, p. 175; figure 21.4). This situation has been clarified by molecular evidence, which shows relationships to be: (Phocidae (Odobenidae + Otariidae)) (Arnason et al. 2006; Higdon et al. 2007). Therefore the scrotal condition in Otariidae is a derived trait within the pinnipeds, and dates to at least ~ 25 Ma, when Odobenidae and Otariidae diverged from one another (Arnason et al. 2006).

In summary, high-level morphological and molecular phylogenies often correspond poorly. Morphological characters are most useful for revealing evolutionary rates and trends, when viewed in the context of stable molecular phylogenies (Springer et al. 2007).

Similar conclusions apply at lower levels of diversification. Many studies have tried to sort out species relationships using male genitalic traits, which often differ conspicuously between related species. Lidicker (1968) used many (66!) diverse traits of phallic soft tissue and the baculum in his phenetic study of New Guinea rodents, but reached only a few clear conclusions: monophyly of the group; the presence of two main clades; and an

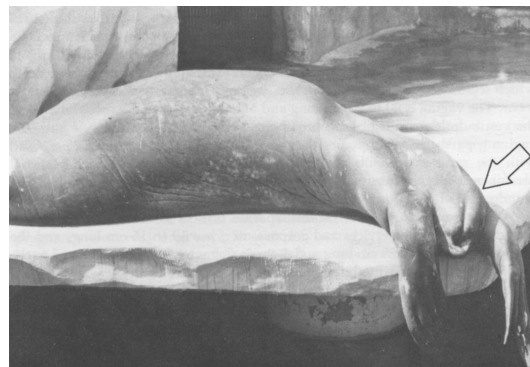


FIGURE 21.4 The walrus (*Odobenus rosmarus*) exhibits a tendency toward scrotal arrangement of the testes, a condition intermediate between seals (Phocidae) and fur seals and sea lions (Otariidae); the walrus is a sister group to the Otariidae. The captive male in the photograph was lying on his back, with body twisted so that the rear end is oriented obliquely toward the viewer. The photograph was taken in March, when the animal was exceptionally lean and testes enlarged. From Fay (1982: figure 108; photograph by G.C. Ray).

Anisomys-like common ancestor. Some of Lidicker's (1968) inferences have been supported by molecular analyses (e.g., *Anisomys* diverged first, within the Australia/New Guinea clade recognized by Steppan et al. [2005]). Therefore some phylogenetic signal is present in genitalic anatomy in this group of rodents; nevertheless, it clearly is too weak to establish a well resolved phylogeny. Therefore, genitalic traits at low levels of divergence are more suitable for character mapping than for phylogenetic inference, as for higher-level analyses. Two examples follow.

REPRODUCTIVE CHARACTER MAPPING AT LOW LEVELS OF DIVERGENCE: THREE EXAMPLES

The Sciuridae is a large and diverse family that includes prairie dogs (*Cynomys*), ground squirrels (*Spermophilus* and other genera), marmots and

groundhogs (*Marmota*), chipmunks (*Tamias* and *Neotamias*), tree squirrels (*Sciurus* and *Tamiasciurus*), and flying squirrels (*Glaucomys*). In a detailed morphological study, Bryant (1945) identified five groups: prairie dogs plus ground squirrels; marmots; chipmunks; tree squirrels; and flying squirrels. These groups (and some higher-level groupings; e.g. "terrestrial squirrels" = prairie dogs, ground squirrels, plus marmots) are identical to those identified on molecular evidence (Herron et al. 2004; Steppan et al. 2004). Molecular analyses have resolved many other relationships: for example, *Spermophilus* ground squirrels are paraphyletic, and *Glaucomys* is the sister group to tree squirrels. Bacular morphology agrees in part with the molecular phylogeny; for example, the baculum is similar between *Cynomys*, *Spermophilus*, and related genera (Wade and Gilbert 1940; Bryant 1945; Burt 1960; figure 21.5). However, discrepancies suggest highly variable divergence rates in bacular morphology and size within some clades. For example,

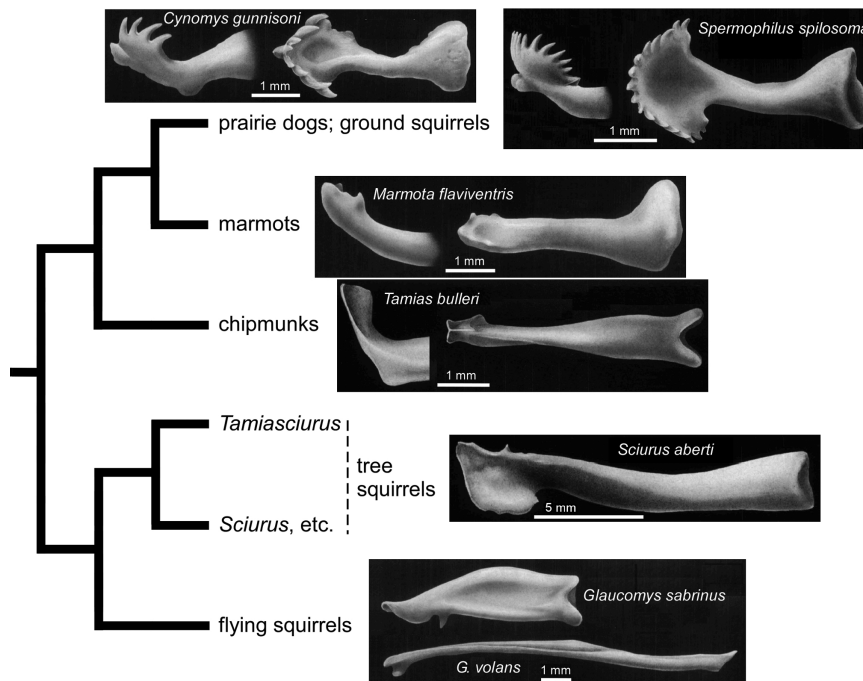


FIGURE 21.5 Character mapping of reproductive traits on a well resolved molecular phylogeny reveals both concordance and discordance. Elaborate claw-like bacula characterize the prairie dog/ground squirrel clade, and a deflected apex occurs in all chipmunks (*Tamias*). However, even bacula of fairly closely related species can differ greatly (e.g., the two species of flying squirrels, *Glaucomys*). Cladogram is based on Herron et al. (2004) and Steppan et al. (2004); illustrations of bacula are from Burt (1960).

the baculum of most tree squirrels is large and complex, but is minute and simple in *Tamiasciurus* (Layne 1952); and the baculum differs greatly between the two *Glaucomys* species (figure 21.5).

Both conservatism and variable divergence rates also characterize the spermatozoa of muroid rodents (= Muridae, Cricetidae, and Nesomyidae). Breed (2004, 2005) mapped spermatozoon characters on a molecular phylogeny, and inferred that the ancestral condition was likely “a sperm head with a bilaterally flattened nucleus ... acrosome-containing apical hook, and long sperm tail” (Breed 2005, p. 289), which occurs in many muroid lineages and also Heteromyidae (an outgroup; figure 21.6). The divergent sperm of *Tatera* (large naked-soled gerbils; Gerbillinae), which diverged from other

Gerbillinae 8–9 Ma, is highly derived (and in fact is unusual within the Mammalia as a whole). *Deomys* and *Lophuromys* sperm also are strongly divergent within the Muridae.

Baryshnikov et al. (2003) carried out a cladistic analysis of the baculum in the Mustelidae and relatives. They detected little phylogenetic information in bacular morphology, but through character mapping could reconstruct the ancestral state and identify some evolutionary trends. Relative size of the baculum is uniform within the group, except it is slightly shorter in the skunks and relatives (Mephitidae). The ancestral baculum was elongate and rod-shaped, with no urethral groove and with a simple apex. More complex morphology is expressed particularly in the apex, in the form of processes, openings, and spoon- or cup-shaped

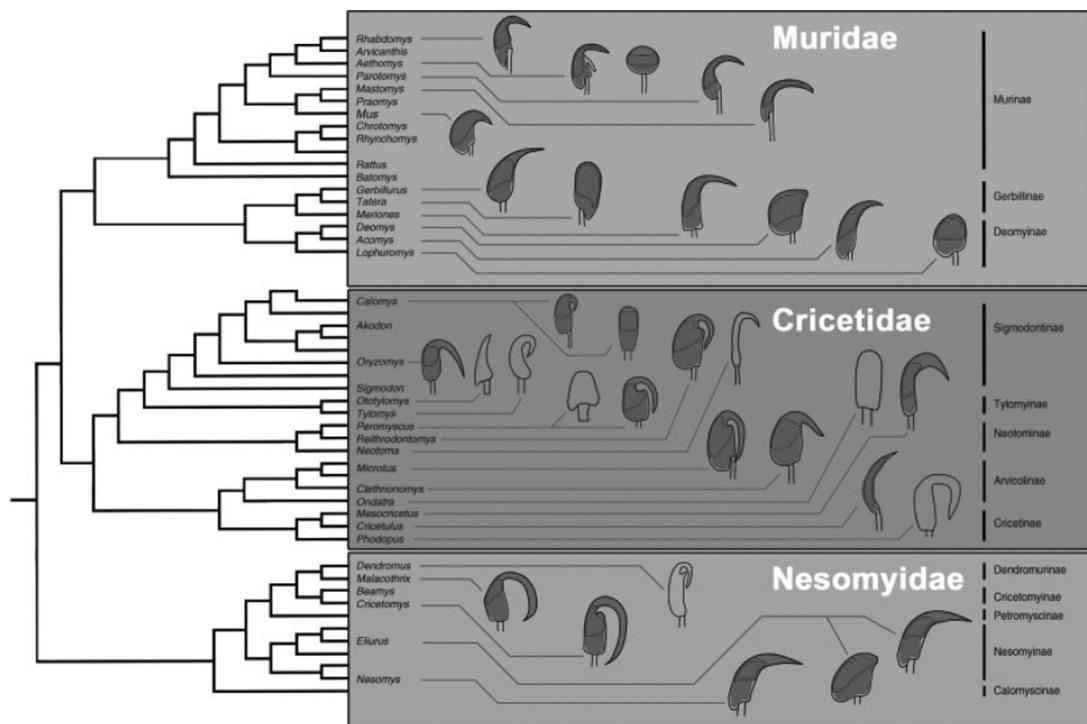


FIGURE 21.6 Character mapping of sperm traits in muroid rodents on a well resolved molecular phylogeny (from Steppan et al. 2004) reveals concordance and discordance, due to great variation in rates of evolutionary divergence. Most species have a sperm head with an apical hook. This hook is largely composed of acrosomal material in most nesomyids, cricetids, and gerbillines, but it contains a nuclear extension with a thinner two-segment acrosome in deomyines and murines. Highly divergent sperm head shapes have evolved that lack an apical hook in a few lineages of most subfamilies (e.g., *Ondatra* [Arvicolinae], two *Habromys* species [Neotominae], one *Calomys* species [Sigmodontinae], African *Tatera* [Gerbillinae], *Lophuromys* [Deomyinae]). From Breed (2005: figure 12).

processes, and the evolution of these specializations within particular lineages could be inferred.

To summarize, character mapping of reproductive traits at fairly low levels of divergence reveals both conservatism and diversification, plus highly variable rates and patterns of divergence (e.g., the baculum of *Tamiasciurus* within tree squirrels, the bacula of the two *Glaucomys* species, and the sperm of *Tatera*). Divergence patterns among related species are especially relevant to how sexual selection, mating systems, and speciation are related.

RELATIONSHIPS OF REPRODUCTIVE ANATOMY TO MATING SYSTEM

Many studies have revealed correlative trends suggesting that the size of male sexual structures is

driven by sexual selection. For example, testis size is related to mating system: testes are relatively small in single-male breeding systems (e.g., monogamy), and relatively large in multi-male systems (e.g., promiscuity), presumably because of frequent copulations and high sperm competition in the latter (Kenagy & Trombulak 1986). In the Cetacea, odontocetes have notably large testes: testes of one harbor porpoise (*Phocoena phocoena*) weighed 2.7 kg, ~6% of body mass (= 45 kg), and “almost as large as ... for a 50-ton fin whale” (Fontaine & Barrette 1997, p. 68). Testes of baleen whales (Mysticeti) are about the expected size for mammals of their size (Kenagy & Trombulak 1986), but within the group, mass of testes is relatively larger in large species (figure 21.7A). In the northern right whale (*Eubalaena glacialis*), combined mass of testes reaches nearly 1000 kg — the largest size both absolutely and relatively (and this is probably an

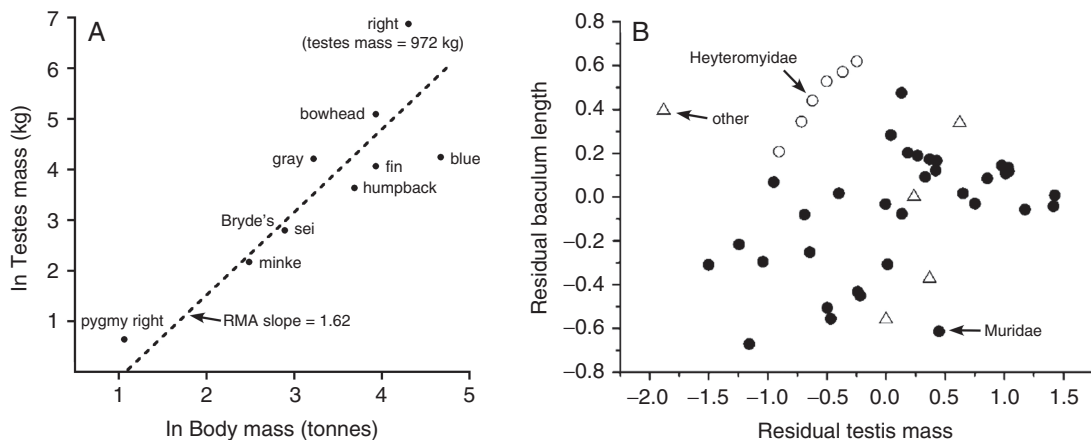


FIGURE 21.7 (A) Early allometric investigations of genital to body size in mammals did not control for phylogeny, but revealed many important patterns. In baleen whales, combined mass of testes (without epididymes) of the northern right whale (*Eubalaena glacialis*) is nearly 1000 kg, which is the largest both absolutely and relatively among baleen whales. Combined mass of testes across species is positively related to body mass, and is characterized by positive allometry (expected slope = 1, for equal proportional change [i.e., isometry] in regression). Scientific names for other species: bowhead *Balaena mysticetus*; blue, *Balaenoptera musculus*; Bryde's, *Balaenoptera edeni*; fin, *Balaenoptera physalus*; gray, *Eschrichtius robustus*; humpback, *Megaptera novaeangliae*; minke *Balaenoptera acutorostrata*; sei, *Balaenoptera borealis*; pygmy right, *Caperea marginata*. (B) Modern analyses control for phylogeny, enabling interspecific trends in relative size of reproductive structures to be evaluated without that complication. This graph is a residual plot of baculum length on testis mass (after controlling for body mass), showing that Muridae tend to have shorter bacula relative to testis size than do Heteromyidae. A few other rodent species are included for comparison. (A) After data in Brownell and Ralls (1986: table 1; those authors incorrectly reported and graphed reduced major axis regression (RMA) slope as 1.35, which is the slope in ordinary least-squares regression). (B) After Ramm (2007: figure 2).

underestimate of size in the breeding period; Brownell & Ralls 1986).³

Early analyses did not control for phylogenetic relationships. Allometric trends like those shown in figure 21.7A are influenced by relationship, because closely related groups tend to be morphologically and behaviorally similar (statistically speaking, the regressions are based on partially correlated data, which violates statistical assumptions and inflates the estimated degrees of freedom; O'Connor et al. 2007). Various methods to control for phylogenetic effects have been proposed (Nunn & Barton 2001; Freckleton et al. 2002). In his phylogenetically controlled analysis, Ramm (2007) found that bacular length and length of glans penis in rodents were both positively related to inferred level of sperm competition (testis mass had a significant and positive effect on both genital size measures in multiple regression analyses, when the influence of body mass was controlled for; figure 21.7B). Relationships differed across groups, suggesting important reproductive differences between Heteromyidae and Muridae.

Size of anatomical structures is related to other factors as well. In terrestrial Carnivora, relative testis size is greatest in species with brief breeding seasons, when synchrony of female estrous and sperm competition are presumed to be highest (Iossa et al. 2008). This relationship is stronger for spontaneous than for induced ovulators (Larivière & Ferguson 2003 present other perspectives). Many other reproductive structures have been investigated, for example, seminal vesicles are largest in primate species presumed to have the most intense sperm competition (with “dispersed” mating systems), and are smallest in monogamous species (Dixson 1998); and the relative size of seminal vesicles and the anterior prostate are positively related to level of sperm competition in rodents (Ramm et al. 2005).

Allometric trends are strongest at high levels of differentiation, and weaken progressively over lower levels of differentiation, such as across conspecific populations or among individuals within populations (Ramm 2007). Nevertheless, trends are apparent and require separate explanations over all scales of divergence. Intraspecific patterns can be particularly informative about relationships between sexual selection and population divergence.

INTRASPECIFIC PATTERNS: GEOGRAPHIC VARIATION

Sexual-selection theory predicts higher variation in sexually-selected traits than in non-sexually-selected traits, even across conspecific populations (Pomiankowski & Iwasa 1998). Wilkinson and McCracken (2003) investigated geographic variation in testicular size in relationship to mating system in two species of bat. In the Jamaican fruit-eating bat (*Artibeus jamaicensis*) in Panama, males attend harems in hollow trees, but female groups are labile, so females may mate with multiple males. In contrast, female group composition is stable in Mexico. In keeping with this difference, testes from Panama are more than six times the size (volume) of those from Mexico. Substantial size variation also occurs on a smaller spatial scale in bats: testes of Mexican free-tailed bats (*Tadarida brasiliensis*) from four colonies in Texas varied in average volume from ~100 to ~170 mm³, paralleling differences in colony size (100,000 to 4–6 million), which in turn is presumed to be correlated with the intensity of sexual selection via sperm competition.

A second example of geographic variation is testicular size in the spinner dolphin (*Stenella longirostris*; figure 21.8A). A number of forms occur in this widely distributed species, including the distinctive eastern spinner dolphin (*S. l. orientalis*) of the far-eastern tropical Pacific. The so-called “whitebelly spinner dolphin” is a broadly distributed hybrid swarm morphologically intermediate between *orientalis* and spinner dolphins to the west (in Hawaii and the South Pacific). Mature male eastern and whitebelly spinner dolphins differ substantially in external appearance, and in testicular size and activity: in whitebelly spinners, testes are much larger, and more males are sexually active at any one time (as judged by sperm abundance in the epididymides). For example, for specimens with combined mass of the right testis and epididymis ~100–300g, only 9% of eastern spinners had copious sperm in the epididymis, versus 47% of whitebelly spinners (Perrin & Mesnick 2003; figure 21.8B). Based on these trends, Perrin & Mesnick (2003, p. 471) inferred that there is a “gradient from a more polygynous mating system in the eastern form

3. Accounts of Kenagy & Trombulak (1986) and Brownell & Ralls (1986) differ somewhat; I follow the latter.



FIGURE 21.8 (A) The spinner dolphin (*Stenella longirostris*) is geographically variable in body size, shape, and coloration, and in testicular size (also note the conspicuous ventral postanal hump in this large adult male eastern spinner, which is absent in the whitebelly form). (B) The whitebelly form has larger testes, and more whitebelly males have sperm than do eastern males (testis mass range 500–700 g shown as example). (A) Photo by B. Pitman/NOAA Fisheries Service, Southwest Fisheries Science Center, Protected Resources Division; (B) after Perrin and Mesnick (2003: figure 5).

to a more open, promiscuous, or polygynandrous mating system in the whitebelly spinner”.

More complex patterns of geographic variation occur in traits other than size. The baculum and baubellum (os clitoridis) of *Tamias* chipmunks vary interspecifically, so might be expected to also vary geographically within species. This is not the case in two chipmunk species. The Allen’s chipmunk (*T. senex*) and Siskyou chipmunk (*T. siskiyou*) are almost identical morphometrically (in cranial features), and exhibit parallel ecogeographic variation in pelage and morphology over their largely sympatric ranges in the western United States. However, the baculum and baubellum are morphologically uniform within each species across the same range (Sutton and Patterson 2000; figure 21.9). On the surface, this finding is not in accord with conventional sexual-selection theory, but instead agrees with Paterson’s (1993) theory of specific mate-recognition systems, which predicts stability in conspecific mate recognition and attraction, and in sexual behavior throughout a species’ range. Evidence on this point is mixed however, as some studies point to substantial intraspecific geographic variation in sexually-selected structures of mammals and other taxa (Kelly et al. 2000; Møller 1995), in accordance with the presumed importance of sexual selection in facilitating differentiation and speciation (Arnqvist & Rowe 2005; Ritchie 2007). For example, bacula and baubella

vary between genetically distinct allopatric populations of the yellow-pine chipmunk (*T. amoenus*; Good et al. 2003). Similarly, population structure is suggested by non-reproductive traits in the European ground squirrel (*Spermophilus citellus*; Kryštufek & Hrabě 1996) and least chipmunk (*T. minimus*; Sullivan & Petersen 1988), and bacular traits vary concordantly with non-reproductive traits in both cases. More detailed analysis of population structure is needed to clarify how sexual selection contributes to the disparate patterns that have been reported in different studies.

INTRASPECIFIC PATTERNS: WITHIN-POPULATION VARIATION

Morphological variation within populations is of evolutionary interest for many reasons (Darwin 1883; Yablokov 1974; Wright 1978; Hallgrímsson and Hall 2005). In the context of sexual selection, such variation (e.g., ornament size or shape) is of special interest because, as noted above, sexually-selected traits are held to be more variable than non-sexually-selected traits (Long and Frank 1968; Long 1969; Lüpold et al. 2004). A simple example is the baculum of the harp seal (*Pagophilus groenlandicus*), which varies in size more than does the humerus (figure 21.10). Such analyses must take

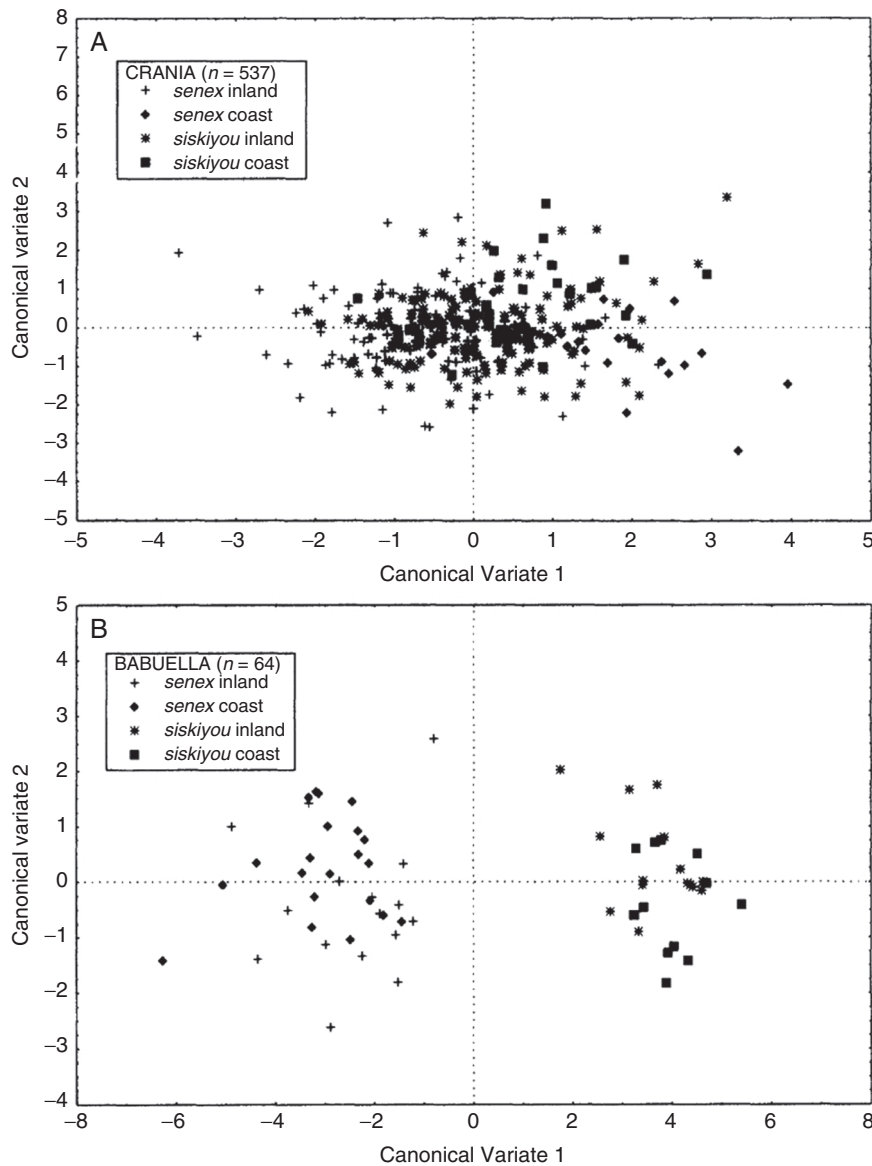


FIGURE 21.9 Two closely related chipmunks (*Tamias senex*, *T. siskiyou*) display parallel ecogeographic variation in body size and coat color across their largely sympatric ranges in the western United States, and are not distinguishable on the basis of cranial variables. However, the baculum and baubellum (os clitoridis) are uniform within and differ distinctively between the species over their distributions. Canonical plots of discriminant function scores are shown for separate analyses on cranial variables (A) and baubellar variables (B). After Sutton and Patterson (2000: figure 3).

social system into account. Two mole-rat (Bathyergidae) species have morphologically differentiated castes, and only a few males reproduce; bacular variation in this case would differ from that in a society where males are more-or-less equivalent;

the same may be true of species in which males have despotic or rank-based access to females (e.g., wolf, *Canis lupus*). The more interesting question in such cases pertains to variation within reproductively active social castes or dominance ranks. Male sea

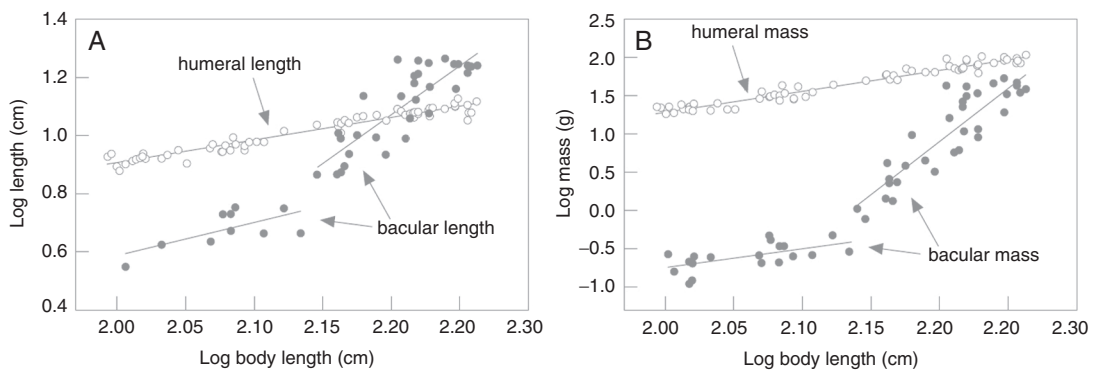


FIGURE 21.10 Sexually-selected traits often are more variable than non-sexually-selected traits within a species. In this study, variation was estimated by residuals from allometric regression (Eberhard et al. 1998; Miller 2009) for size (A, length; B, mass) of the baculum and humerus in the harp seal (*Pagophilus groenlandicus*). From Miller and Burton (2001: figure 2).

lions and fur seals exhibit deferred social maturity, entering the territorial system years after they are physiologically capable of fertilizing females (Miller 2009). Males that are large for their age may become territorial at a younger age (Miller et al. 2000; Roberts 1988; Scheffer 1950); therefore estimates of genitalic (e.g., bacular and testicular) size variation within age classes will be biased upward if territorial and non-territorial males of the same age are not represented proportionately in the samples. Wilkinson & McCracken (2003) made a similar point for bats.

Levels of variation in homologous reproductive structures may differ between males and females. The baubellum appears to be more variable than the baculum in size and morphology, although it is morphologically complex in some species (e.g., *Sciurus* tree squirrels; Layne 1954; Long and Frank 1968). As noted above, the baculum of *Tamiasciurus* tree squirrels is tiny and simple, and the baubellum is only variably present (Layne 1952). The baubellum is similarly small and variably present in the walrus, and even becomes smaller with age; yet this species has the largest baculum of any species of mammal, both absolutely and relatively (Mohr 1963; Fay 1982; Dixson 1995; figure 21.11). Such observations will remain uninterpretable until baubellar function is clarified.

Sexual recognition and mating in mammals entail all senses, and involve components of biochemistry, physiology, behavior, and morphology. It seems unlikely that sexually-selected traits would show similar patterns in variation across such a

range of systems. For example, display behavior and structures may be free to vary a fair amount, whereas size and shape of the penis and vagina must be constrained simply because of the need for morphological compatibility during intromission and copulation (Paterson 1993; Eberhard et al. 1998; Froehlich 2003; Hosken & Stockley 2004; McPeck et al. 2008). If so, one can predict a positive relationship in reproductive size traits between the sexes.

In deer mice (*Peromyscus*), bacular and vaginal lengths are positively correlated both inter- and intraspecifically (Patterson and Thaler 1982; figure 21.12A). Kinahan et al. (2007) reported that both bacular and vaginal lengths scale positively on body size in the Cape dune mole-rat (*Bathyergus suillus*). In *Tamiasciurus*, males have a long, filiform penis, and estrous females have a long coiled vagina, unlike other tree squirrels; other examples of intersexual concordance in rodents are given by Patterson & Thaler (1982). Some recent analyses have revealed repeated patterns of male-female coevolution. Anderson et al. (2006) investigated coevolution of sexual traits in the context of sperm competition in 48 species. They posited that length of the oviduct should increase with the intensity of sperm competition. In phylogenetically controlled analyses, they found that oviduct length was positively related to two measures known in turn to be positively correlated with intensity of sperm competition: relative testes volume and sperm midpiece volume (Anderson et al. 2005; figure 21.12B). Such examples could be multiplied and extended to other

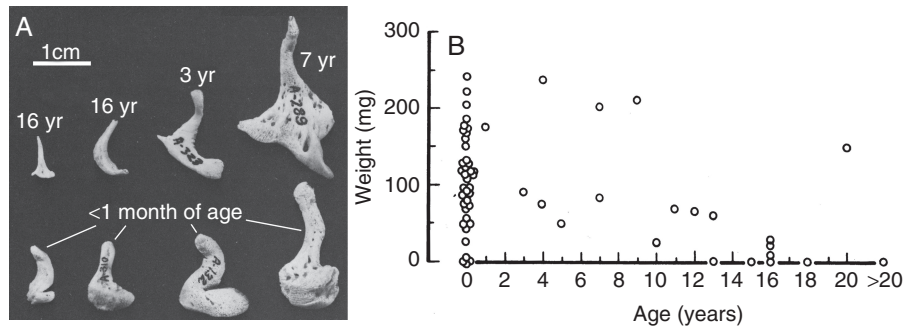


FIGURE 21.11 The baculum of the walrus (*Odobenus rosmarus*) is the largest in mammals, both in absolute size and relative to body size; as in other mammals, it increases in size with age. The species' os clitoridis is small (sometimes it is absent) and morphologically unlike the baculum, and tends to decline in size with age. (A) Clitoris bones from Pacific walruses (*Odobenus rosmarus divergens*) of various ages. (B) The clitoris bone tends to decrease in mass with age; dry mass of calcified tissue is plotted on the Y-axis. After Fay (1982: figures 26 and 27).

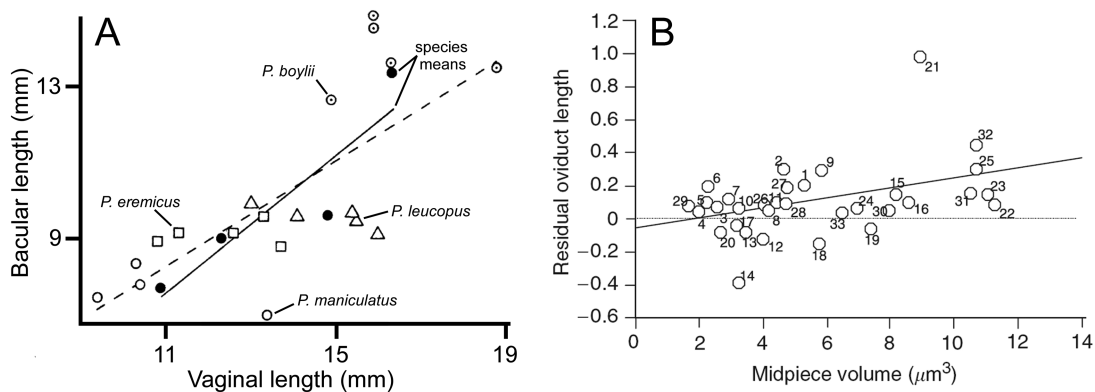


FIGURE 21.12 Concordance between male and female reproductive traits reflects coevolution between the sexes. (A) Size of male and female reproductive structures are positively correlated across populations and species of deer mice (*Peromyscus*). Multiple symbols for each species represent samples from different sites within the state sampled (New Mexico). (B) Length of the oviduct is positively related to midpiece volume of the sperm across species, suggesting coevolution through the action of sexual selection. (A) After Patterson and Thaler (1982: figure 3); (B) After Anderson et al. (2006: figure 1b).

taxa (Eberhard 1996; Brennan et al. 2007; Rönn et al. 2007).

Parallel evolution of male and female reproductive traits can come about in various ways, but rarely through cooperative evolution (Eberhard 1996, 2004a, b, 2006; Arnqvist & Rowe 2005). Simple patterns in genitalic size, as in the examples above, sometimes must merely reflect correlated change to ecogeographic variation in body size (Kitchener et al. 1994). Others result from adaptive

changes in males to changing reproductive traits of females. In the chimpanzee (*Pan troglodytes*), the female's sexual skin swelling substantially increases the distance a male must penetrate in order to achieve fertilization, which may have led to the evolution of the male's elongated, filiform penis (Dixson & Mundy 1994). Similar explanations may apply to *Tamiasciurus* and many other species. Other evolutionary changes in males are responses to competitive conditions created by the mating

system, or by females themselves (e.g., females may cluster in space or time, or have a lengthy estrus). Some such evolutionary responses are mentioned above (e.g., the large testes of the northern right whale and the whitebelly form of the spinner dolphin). Another is the enhanced mechanism of seminal coagulation and copulatory plug formation in primates with high levels of sperm competition (Dixson & Anderson 2002).

DERIVED ROLES OF GENITALIA IN COMMUNICATION

Essentially all aspects of sexual interaction between males and females entail communication, including: looking at, smelling, or touching genitals; testing urine; mounting; and physical and chemical interactions within the female during intromission (Dewsbury 1988). Each sex provides a richness of cues to the other sex. Many unspecialized morphological and behavioral cues have evolved into formalized displays and interactive behavior through ritualization (Tinbergen 1952; Immelmann & Beer 1989). For example, many endocrine-associated traits have been co-opted for signaling; the best known example is cyclical change in the sexual skin of some Old World primates. Specialized markings on or around the genitals and nipples of male and female primates also have evolved for signaling (Dixson 1998; Gerald 2003; Zinner et al. 2004). Much sexual communication takes place over short distances, and so less striking genitalic features can

provide valuable information to receivers. For example, at the beginning of sexual activity in females of the greater dwarf lemur (*Cheirogaleus major*), the genital region, “including the clitoris, becomes turgescient and pink, the vaginal opening appears and the ventral side of the clitoris itself opens completely” (Petter-Rousseaux 1964, pp. 112–113; figure 21.13). Similarly subtle morphological changes take place in estrus of some pinnipeds (Miller 1991).

Some variation in morphological traits is informative about age or social rank. The penis and scrotum in the vervet monkey (*Cercopithecus aethiops*) are strikingly colored and highly variable across males, and are important in static and dynamic optical displays. In this species, males with dark scrota dominate males with paler scrota, and more antagonism occurs between males with similarly dark or pale scrota (Gerald 2001, 2003). The scrotum of the northern brown bandicoot (*Isodon macrourus*) becomes increasingly pigmented with age, so could provide socially useful information to conspecific males or females (Gemmell 1987). The scrotum of the Geoffroy’s spider monkey (*Ateles geoffroyi*) is variably pigmented, and pigmentation may increase with age in this species too (Gerald 2003). The scrotum is vivid blue in males of several marsupial species, a feature that has arisen independently at least twice (Prum & Torres 2004); presumably scrotal color is important in optical signaling, but its relationship to rank and age is unknown.

Intraspecific social mimicry of males by females is common, for example in plain-dwelling cursorial

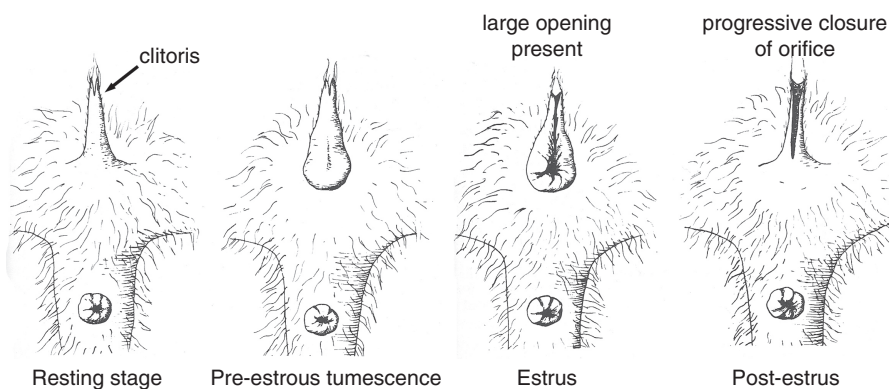


FIGURE 21.13 Physiological changes associated with reproduction often produce changes in appearance, many of which have been co-opted for purposes of optical communication. Females of the greater dwarf lemur (*Cheirogaleus major*) show conspicuous genitalic changes over the reproductive cycle that may function in optical communication. After Petter-Rousseaux (1964: figure 10).

ungulates (Wickler 1968; Geist 1998). Genital mimicry (“andromimicry”; Estes 1991) is part of this syndrome. The best known example is the spotted hyaena (*Crocuta crocuta*), in which andromimicry likely evolved to reduce inter-female aggression (Muller & Wrangham 2002). This has resulted in dramatic anatomical reshaping of the female, with equally dramatic functional consequences: the labia fuse during fetal life to form a pseudo-scrotum, so females lack an external vagina; and the clitoris is enlarged and approximates the size and shape of the penis, and can be erected like the penis. During intromission, the penis enters the clitoral meatus and becomes positioned in the clitoral portion of the urogenital canal (in addition, the fairly large (1.1–1.6 kg) precocial infants are born through the clitoris (Cunha et al. 2003)). Andromimicry involving the genitalia also is known for long-tailed macaques (*Macaca fascicularis*), in which females

develop a pseudoscrotum (Malaijijitnon et al. 2007), and for the Bovidae (Estes 1974, 1991). Yearling female wildebeest (*Connochaetes gnu*) develop (and maintain through adulthood) “hair and adipose tissue resembling the tip of the penile sheath”, and females in the Ankole breed of cattle (*Bos taurus*) “develop a conspicuous penile flap resembling that of a subadult male except for the long hairs” (Estes 1991, p. 436; figure 21.14).

Many optical, chemical, and acoustic cues are available to receivers, but are not given through specialized display behavior. Others are provided through fairly simple motor patterns such as approach, touching, or presentation — behavior which can nevertheless be highly structured. Presentation by female Old World primates is an example; it is performed even by females of species that lack sexual swellings (Wickler 1967). Similarly, tactile communication involving the genitals is

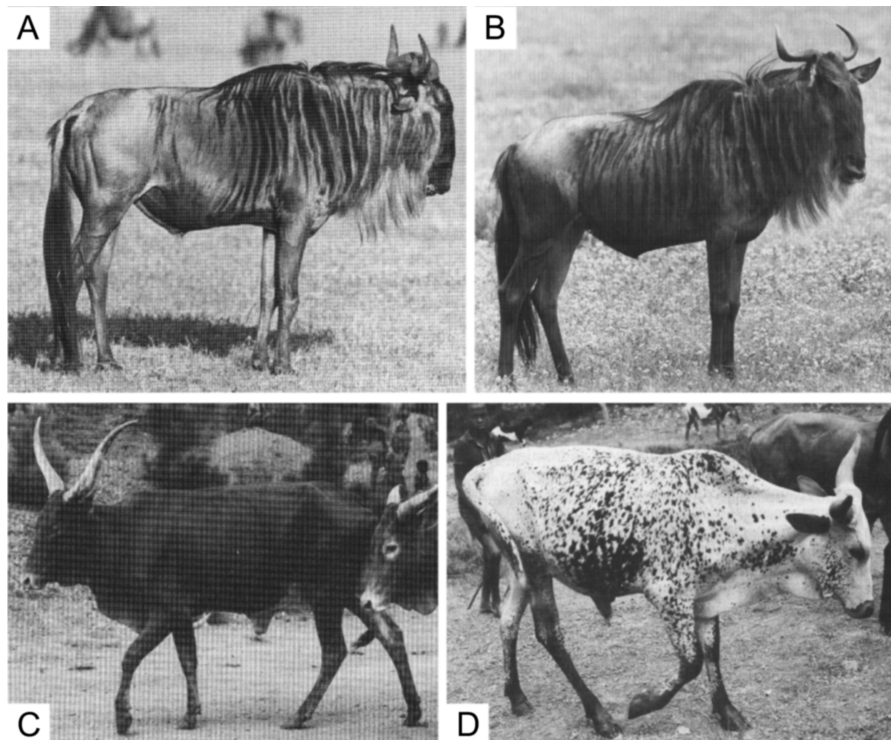


FIGURE 21.14 Mimicry of males by females (“andromimicry”) occurs in many mammals, and includes examples of mimicry of the external genitalia. A and B, Adult male and female wildebeest (respectively) (*Connochaetes gnu*), showing female’s well developed “penile” tuft. C and D, Subadult male and adult female (respectively) Ankole cattle (*Bos taurus*); note similarity between sexes in “penile” flap and dewlap. From Estes (1991: figures 8A, 8B, 9B, and 9A, respectively).

highly structured, and occurs in all mammals; genitals can be contacted with the manus, mouth, tongue, or nose. Extensive tactile communication occurs in the bonobo (*Pan paniscus*), including genito-genital rubbing between females (de Waal 1988; figure 21.15).

Specialized postures or movements by the sender, or complex interactions, commonly accompany morphological and other display specializations. Males of many Old World primate species display their genitals while sitting with legs spread (figure 21.16). In two species of baboon (*Papio*), the bright pink penis is conspicuous against the dark pelage, and in the vervet monkey, “the penis is usually erected ... and may be repeatedly struck against the stomach with a jerky action” (Wickler 1967, p. 150), making the brightly colored genitals even more conspicuous. The genitals are used in other displays of this species as well⁴. One aggressive display between male guinea pigs (*Cavia porcellus*) is sudden extrusion of the testicles directed toward the other animal (Kunkel & Kunkel 1964). The reverse occurs in rhesus macaques: adult males may retract their testes into the inguinal canal when approached closely or frightened by a dominant individual (Altmann 1962).

To summarize, reproductive morphology of mammals is used extensively in and has become specialized in many ways for purposes of sociosexual communication. Many conspicuous optical specializations have been recognized, but far less attention has been given to less striking optical signals, to tactile signals, or to signaling and interactive behavior themselves.

CONCLUSIONS AND SUGGESTIONS FOR FURTHER RESEARCH

Mammalian genitals do not exist in isolation, and have not evolved as functionally isolated entities that serve only in reproduction. Genitals have

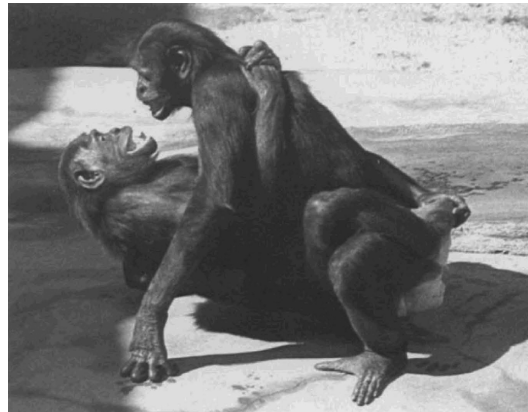


FIGURE 21.15 The genitals are involved in many forms of tactile communication in mammals. This photograph shows two female bonobos (*Pan paniscus*) engaged in genito-genital rubbing. From de Waal (1988: figure 11C).

multiple functions within species and divergent functions across species, and are embedded within integrated morphological–physiological–behavioral systems (Simmons & Jones 2007). Therefore to understand patterns of diversity like those touched on in this chapter, integrated research that cuts across levels of biological organization and scientific disciplines is needed.

Many significant patterns have been revealed by recent research on genitalic diversity in relation to sexual selection and mating system, such as male–female coevolution, and relationships of size and morphology of sexual structures to mating system. At the same time, the generality of many studies means that we lack insight into which mechanisms are responsible for trends and for exceptions to trends. The varied reports on intraspecific geographic variation in bacula are an example (see above). In a similar vein, why are bacular and cranial traits taxonomically concordant in identifying taxonomic groups within one subgenus (*Proechimys*) of spiny rats *Proechimys*, but discordant in another

4. “In *C. a. pygerythrus*, the blue scrotum is displayed to conspecific males and females during a variety of agonistic, dominance and intergroup territorial displays ... The blue scrotum is featured prominently in the ‘red-white-and-blue’ display that combines the bright red penis, the white belly fur and skin and the blue scrotum; in the red-white-and-blue display, a dominant male walks around a submissive male with his tail raised, displaying his blue scrotum ... Sometimes during the red-white-and-blue-display, a male stands upright with his erect penis bobbing up and down ... frequency of performance of the red-white-and-blue display is correlated with dominance and mating success ...” Prum & Torres (2004, p. 2168).

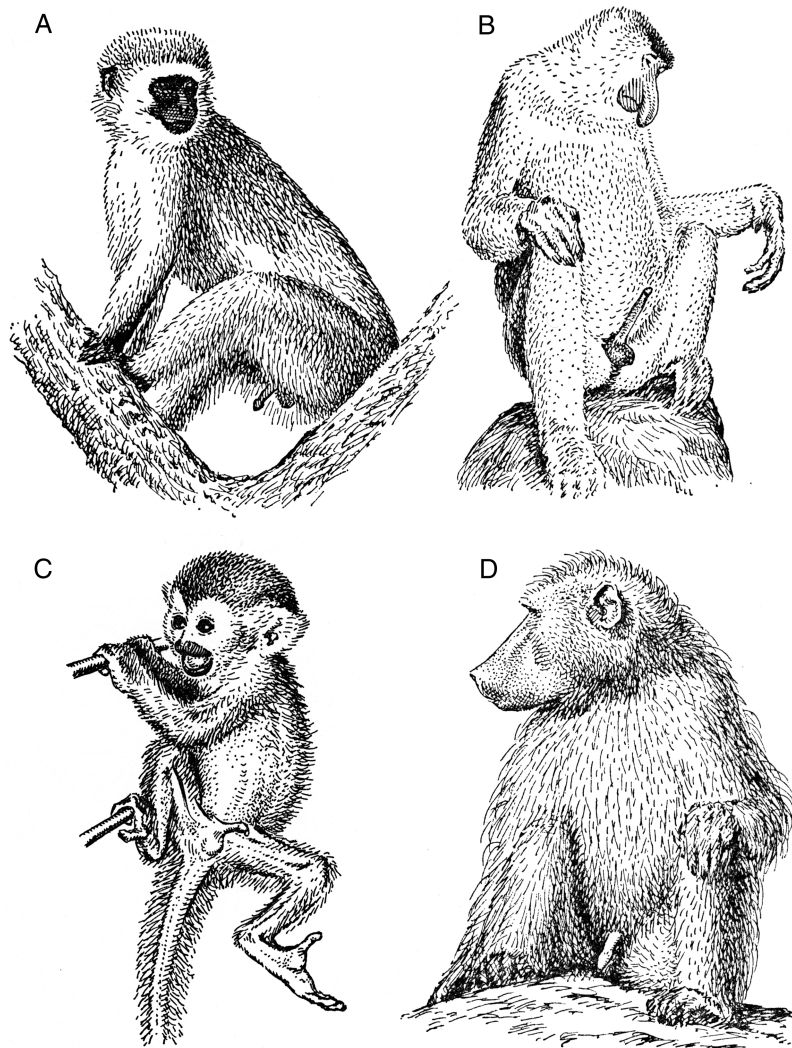


FIGURE 21.16 Many optical displays of primates involve the genitals. (A) Adult male vervet monkey (*Cercopithecus aethiops*). (B) Adult male proboscis monkey (*Nasalis larvatus*). (C) Young squirrel monkey (*Saimiri sciurus*). (D) Adult male olive baboon (*Papio anubis*). After Wickler (1967: figures 11C and 12A, B, D).

(*Trinomys*), in which only the bacula are species-distinctive (Pessôa & dos Reis 1992)? More detailed research is called for in other cases too. For example, in their study of North American voles (*Microtus*; *Clethrionomys*), Heske & Ostfeld (1990) found relatively small testes in polygynous and male-territorial species, and relatively large testes in promiscuous species, but paradoxically large testes also characterized socially monogamous

species. Such findings could be illuminated through detailed functional and behavioral studies.

Recent morphological and functional analyses invite a comparative approach. The mammalian penis is inflatable and stiff (i.e., resistant to bending), design features that may be achievable in only a limited number of ways (Kelly 2002, 2004, 2008). The role of the baculum in erection has been investigated for the Norway rat (*Rattus norvegicus*;

Kelly 2000). The baculum of this species is load-bearing, and transfers forces from the distal glans to the walls of the corpus cavernosum, with the eventual effect of increasing penile stiffness. The baculum of the Norway rat lies well within penile soft tissue and is morphologically simple, unlike many species: position within the penis, morphology, and size vary greatly among rodents (Burt 1960; Patterson 1983; figure 21.1). In some species, the bacular apex is large, simple, and inflected, and lies close beneath the surface of the glans (figure 21.1C); in others, the apex is morphologically complex and multipartite (figure 21.1D), and in others it lies more deeply and a cartilaginous cap projects to beneath the glans (figure 21.1E); and so on. Such great variation must translate into appreciable functional differences interspecifically, even within single taxonomic groups. Dewsbury (1975) called for integrated studies on morphology and copulatory behavior, and this recent work offers opportunities for doing so; the role of the female in copulation needs to be included in such a program.

Comparative behavioral studies likewise are essential for revealing display functions of and phylogenetic diversification of specialized genital morphology, and in turn advancing understanding of how sexual selection operates in different populations and species. Chemical communication by

products of genitalic glands or of glands that are near the genitals, or by products in urine and feces, offers many possibilities. Again, the role of the female in communication needs to be given increased attention — in addition to being involved from initial recognition through to copulation, females also play important roles in postmating events, through cryptic internal selection (Eberhard 1996) to physical removal of copulation plugs (Koprowski 1992).

Mammals have morphologically diverse, complex genitalia, whose functional diversity is just starting to be documented and interpreted in evolutionary terms. The short-beaked echidna (*Tachyglossus aculeatus*) has an anatomically remarkable penis, with a bifid glans and urethra as in monotremes and most marsupials (unifid in some derived marsupials; Smith & Madkour 1980). Each part of the urethra bifurcates further, terminating in two epidermal rosettes. All four rosettes are prominent in early erection, but those on one side retract in later erection, leaving only two to transmit semen to one of the female's oviductal ostia (Johnston et al. 2007; figure 21.17A). This pattern of erection and sperm transmission resembles the use of hemipenes by squamates. Many other mysteries about genital form, function, and evolution in mammals remain (figure 21.17B).

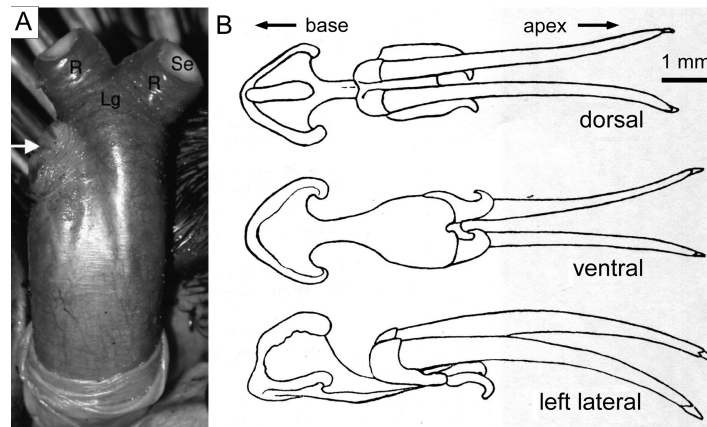


FIGURE 21.17 Mammalian genitalia are complex in form and function. (A) Fully erect penis of short-beaked echidna (*Tachyglossus aculeatus*), in ventral view, showing one-sided retraction of the two terminal rosettes on the right side (arrow). The right side is erect, and semen is visible, pooled in the rosette openings (Lg, left glans; R, rosettes; Se, semen). (B) Morphologically bizarre baculum of the greater Egyptian jerboa (*Jerboa orientalis*). (A) After Johnston et al. (2007: figure 2); (B) From Didier and Petter (1960: figure 3).

Acknowledgments I thank the many people who have helped me with this chapter, by providing literature, illustrations, criticisms, advice, support, and inspiration: W. G. Breed, W. G. Eberhard, the late F. H. Fay, M. Gonzalez-Fideli, D. A. Kelly, S. L. Mesnick, W. F. Perrin, B. D. Patterson, G. C. Ray, M. S. Springer, and S. J. Steppan. During the preparation of this chapter, my research has been supported by the Natural Sciences and Engineering Research Council of Canada.

REFERENCES

- Altmann, S. A. 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. *Annals of the New York Academy of Sciences*, 102, 338–435
- Anderson, M. J., Nyholt, J. & Dixson, A. S. 2005. Sperm competition and the evolution of sperm midpiece volume in mammals. *Journal of Zoology*, 267, 135–142.
- Anderson, M. J., Dixson, A. S. & Dixson, A. F. 2006. Mammalian sperm and oviducts are sexually selected: evidence for co-evolution. *Journal of Zoology*, 270, 682–686.
- Arnason, U., Gullberg, A., Janke, A., Kullberg, M., Lehman, N., Petrov, E. A. & Väinölä, R. 2006. Pinniped phylogeny and a new hypothesis for their origin and dispersal. *Molecular Phylogenetics and Evolution*, 41, 345–354.
- Arnqvist, G., & Rowe, L. 2005. *Sexual Conflict*. Princeton, New Jersey: Princeton University Press.
- Baryshnikov, G. F., Bininda-Emonds, O. R. P. & Abramov, A. V. 2003. Morphological variability and evolution of the baculum (os penis) in Mustelidae (Carnivora). *Journal of Mammalogy*, 84, 673–690.
- Bedford, J. M., Mock, O. B. & Goodman, S. M. 2004. Novelty of conception in insectivorous mammals (Lipotyphla), particularly shrews. *Biological Reviews*, 79, 891–909.
- Berta, A. & Wyss, A. R. 1994. Pinniped phylogeny. *Proceedings of the San Diego Society of Natural History*, 29, 33–56.
- Breed, W. G. 2004. The spermatozoon of Eurasian murine rodents: its morphological diversity and evolution. *Journal of Morphology*, 261, 52–69.
- Breed, W. G. 2005. Evolution of the spermatozoon in muroid rodents. *Journal of Morphology*, 265, 271–290.
- Brennan, P. L. R., Prum, R. O., McCracken, K. G., Sorenson, M. D., Wilson, R. E. & Birkhead, T. R. 2007. Coevolution of male and female genital morphology in waterfowl. *PLoS ONE*, 2, e418.
- Brownell Jr., R.L. & Ralls, K. 1986. Potential for sperm competition in baleen whales. Report of the International Whaling Commission Special Issue, 8, 97–112.
- Bryant, M. D. 1945. Phylogeny of Nearctic Sciuridae. *American Midland Naturalist*, 33, 257–390.
- Burt, W. H. 1960. *Bacula of North American mammals*. Miscellaneous Publications, Museum of Zoology, University of Michigan, 113, 1–76 + 25 plates.
- Carleton, M. D., Hooper, E. T. & Honacki, J. 1975. Karyotypes and accessory reproductive glands in the rodent genus *Scotinomys*. *Journal of Mammalogy*, 56, 916–921.
- Coleman, W. 1964. *Georges Cuvier, Zoologist. A Study in the History of Evolution Theory*. Cambridge, Massachusetts: Harvard University Press.
- Cunha, G. R., Wang, Y., Place, N. J., Liu, W., Baskin, L. & Glickman, S. E. 2003. Urogenital system of the spotted hyena (*Crocuta crocuta Erxleben*): a functional histological study. *Journal of Morphology*, 256, 205–218.
- Darwin, C. 1883. *The Variation of Animals and Plants Under Domestication*. Second rev. ed. New York: D. Appleton and Co.
- De Waal, F. B. M. 1988. The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. *Behaviour*, 106, 183–251.
- Dewsbury, D. A. 1975. Diversity and adaptation in rodent copulatory behavior. *Science*, 190, 947–954.
- Dewsbury, D. A. 1988. Copulatory behavior as courtship communication. *Ethology*, 79, 218–234.
- Didier, R. & Petter, F. 1960. L'os pénien de *Jaculus blanfordi* (Murray) 1884 (sic) étude comparée de *J. blanfordi*, *J. jaculus* et *J. orientalis* (rongeurs, dipodidés). *Mammalia*, 24, 171–176.
- Dixson, A. F. 1995. Baculum length and copulatory behaviour in carnivores and pinnipeds (Grand Order Ferae). *Journal of Zoology*, London, 235, 67–76.
- Dixson, A. 1998. *Primate Sexuality. Comparative Studies of the Prosimians, Monkeys, Apes,*

- and Human Beings. Oxford, England: Oxford University Press.
- Dixson, A. F. & Anderson, M. J. 2002. Sexual selection, seminal coagulation and copulatory plug formation in Primates. *Folia Primatologica*, 73, 63–69.
- Dixson, A. F. & Mundy, A. I. 1994. Sexual behavior, sexual swelling, and penile evolution in chimpanzees (*Pan troglodytes*). *Archives of Sexual Behavior*, 23, 267–280.
- Dobzhansky, T. 1970. *Genetics of the Evolutionary Process*. New York: Columbia University Press.
- Eberhard, W. G. 1985. *Sexual Selection and Animal Genitalia*. Cambridge, Massachusetts: Harvard University Press.
- Eberhard, W. G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice*. Princeton, New Jersey: Princeton University Press.
- Eberhard, W. G. 2004a. Male–female conflict and genitalia: failure to confirm predictions in insects and spiders. *Biological Reviews*, 79, 121–186.
- Eberhard, W. G. 2004b. Rapid divergent evolution of sexual morphology: comparative tests of antagonistic coevolution and traditional female choice. *Evolution*, 58, 1947–1970.
- Eberhard, W. 2006. Sexually antagonistic coevolution in insects is associated with only limited morphological diversity. *Journal of Evolutionary Biology*, 19, 657–681.
- Eberhard, W. G., Huber, B. A., Rodriguez S., R. L., Briceño, R. D., Salas, I. & Rodriguez, V. 1998. One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. *Evolution*, 52, 415–431.
- Estes, R. D. 1974. Social organization of the African Bovidae. In: *The Behaviour of Ungulates and its Relation to Management*. New Series No. 24 (Ed. by V. Geist & F. Walther), pp. 166–205. Morges, Switzerland: International Union for the Conservation of Nature.
- Estes, R. D. 1991. The significance of horns and other male secondary sexual characters in female bovids. *Applied Animal Behaviour Science*, 29, 403–451.
- Fay, F. H. 1982. Ecology and biology of the Pacific walrus, *Odobenus rosmarus divergens* Illiger. *North American Fauna*, 74, 1–279.
- Findley, J. S. 1968. Insectivores and dermopterans. In: *Recent Mammals of the World. A Synopsis of Families* (Ed. By Anderson, S. & J. Knox Jones Jr.), pp. 87–108. New York: Ronald Press.
- Fontaine, P. M. & Barrette, C. 1997. Megatestes: anatomical evidence for sperm competition in the harbor porpoise. *Mammalia*, 61, 65–71.
- Freckleton, R. P., Harvey, P. H. & Pagel, M. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. *American Naturalist*, 160, 712–726.
- Froehlich, J. W. 2003. Testing some theoretical expectations of sexual selection versus the recognition concept in the speciose macaques of Sulawesi, Indonesia. In: *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. Special Topics in Primatology, vol. 3 (Ed. by C. B. Jones), pp. 539–591. Norman, Oklahoma: American Society of Primatologists.
- Gaeth, A. P., Short, R. V. & Renfree, M. B. 1999. The developing renal, reproductive, and respiratory systems of the African elephant suggest an aquatic ancestry. *Proceedings of the National Academy of Sciences of the USA*, 96, 5555–5558.
- Geist, V. 1998. *Deer of the World: Their Evolution, Behavior, and Ecology*. Mechanicsburg, Pennsylvania: Stackpole Books.
- Gemmell, R. T. 1987. Sexual maturity in the captive male bandicoot, *Isodon macrourus*. *Australian Journal of Zoology*, 35, 433–441.
- Gerald, M. S. 2001. Primate colour predicts social status and aggressive outcome. *Animal Behaviour*, 61, 559–566.
- Gerald, M. S. 2003. How color may guide the primate world: possible relationships between sexual selection and sexual dichromatism. In: *Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions*. Special Topics in Primatology, vol. 3 (Ed. by C. B. Jones), pp. 141–172. Norman, Oklahoma: American Society of Primatologists.
- Good, J. M., Demboski, J. R., Nagorsen, D. W. & Sullivan, J. 2003. Phylogeography and introgressive hybridization: chipmunks (genus *Tamias*) in the northern Rocky Mountains. *Evolution*, 57, 1900–1916.

- Gottreich, A., Hammel, I., Yogeve, L., Bartoov, B. & Terkel, J. 2001. Structure and function of accessory sex glands in the male blind mole rat (*Spalax ehrenbergi*). *Journal of Mammalogy*, 82, 201–208.
- Gowaty, P. A. 1997. Sexual dialectics, sexual selection, and variation in reproductive behavior. In: *Feminism and Evolutionary Biology: Boundaries, Intersections, and Frontiers* (Ed. by P. A. Gowaty), pp. 351–384. New York: Chapman and Hall.
- Hall, B. K. (Ed.) 1994. *Homology: the Hierarchical Basis of Comparative Biology*. San Diego, California: Academic Press.
- Hallgrímsson, B. & Hall, B. (Eds.) 2005. *Variation: a Central Concept in Biology*. Burlington, Massachusetts: Elsevier Academic Press.
- Herron, M. D., Castoe, T. A. & Parkinson, C. L. 2004. Sciurid phylogeny and the paraphyly of Holarctic ground squirrels (*Spermophilus*). *Molecular Phylogenetics and Evolution*, 31, 1015–1030.
- Heske, E. J., & Ostfeld, R. S. 1990. Sexual dimorphism in size, relative size of testes, and mating systems in North American microtine rodents. *Journal of Mammalogy*, 71, 510–519.
- Higdon, J. W., Bininda-Emonds, O. R. P., Beck, R. M. D. & Ferguson, S. H. 2007. Phylogeny and divergence of the pinnipeds (Carnivora: Mammalia) assessed using a multigene dataset. *BMC Evolutionary Biology*, 7–216.
- Hooper, E. T. 1960. The glans penis in *Neotoma* (Rodentia) and allied genera. *Occasional Papers of the Museum of Zoology, University of Michigan*, 618, 1–21 + 11 plates.
- Hosken, D. J. & Stockley, P. 2004. Sexual selection and genital evolution. *Trends in Ecology and Evolution*, 19, 87–93.
- Huxley, T. H. 1864. *Lectures on the Elements of Comparative Anatomy*. London, England: John Churchill and Sons.
- Immelmann, K. & Beer, C. 1989. *A Dictionary of Ethology*. Cambridge, Massachusetts: Harvard University Press.
- Iossa, G., Soulsbury, C. D., Baker, P. J. & Harris, S. 2008. Sperm competition and the evolution of testes size in terrestrial mammalian carnivores. *Functional Ecology*, 22, 655–662.
- Johnston, S. D., Smith, B., Pyne, M., Stenzel, D. & Holt, W. V. 2007. One-sided ejaculation of echidna sperm bundles. *American Naturalist*, 170, E162–E164.
- Kelly, C. D., Godin, J. J.-G. & Abdallah, G. 2000. Geographical variation in the male intromittent organ of the Trinidadian guppy (*Poecilia reticulata*). *Canadian Journal of Zoology*, 78, 1674–1680.
- Kelly, D. A. 2000. Anatomy of the baculum-corporis cavernosum interface in the laboratory rat (*Rattus norvegicus*), and implications for force transfer during copulation. *Journal of Morphology*, 244, 69–77.
- Kelly, D. A. 2002. The functional morphology of penile erection: tissue designs for increasing and maintaining stiffness. *Integrative and Comparative Biology*, 42, 216–221.
- Kelly, D. A. 2004. Turtle and mammal penis designs are anatomically convergent. *Proceedings of the Royal Society, Biology Letters*, 271 (Suppl 5), S293–S295.
- Kelly, D. A. 2008. Penises as variable-volume hydrostatic skeletons. *Annals of the New York Academy of Sciences*, 1101, 453–463.
- Kenagy, G. J. & Trombulak, S. C. 1986. Size and function of mammalian testes in relation to body size. *Journal of Mammalogy*, 67, 1–22.
- Kinahan, A., Bennett, N., O’Riain, M., Hart, L. & Bateman, P. 2007. Size matters: genital allometry in an African mole-rat (Family: Bathyergidae). *Evolutionary Ecology*, 21, 201–213.
- Kitchener, D. J., Adams, M. & Boeadi. 1994. Morphological and genetic relationships among populations of *Scotorepens sanborni* (Chiroptera: Vespertilionidae) from Papua New Guinea, Australia and Indonesia. *Australian Mammalogy*, 17, 31–42.
- Koprowski, J. L. 1992. Removal of copulatory plugs by female tree squirrels. *Journal of Mammalogy*, 73, 572–576.
- Kryštufek, B. & Hrabě, V. 1996. Variation in the baculum of the European souslik, *Spermophilus citellus*. *Zeitschrift für Säugetierkunde*, 61, 228–235.
- Kunkel, P. & Kunkel, I. 1964. Beiträge zur Ethologie des Hausmeerschweinchens *Cavia aperea f. porcellus* (L.). *Zeitschrift für Tierpsychologie*, 21, 602–641.
- Larivière, S., & Ferguson, S. H. 2003. Evolution of induced ovulation in North American carnivores. *Journal of Mammalogy*, 84, 937–947.
- Layne, J. N. 1952. The os genitale of the red squirrel, *Tamiasciurus*. *Journal of Mammalogy*, 33, 457–459.

- Layne, J. N. 1954. The os clitoridis of some North American Sciuridae. *Journal of Mammalogy*, 35, 357–366.
- Lidicker Jr., W. Z. 1968. A phylogeny of New Guinea rodent genera based on phallic morphology. *Journal of Mammalogy*, 49, 609–643.
- Long, C. A. 1969. Gross morphology of the penis in seven species of the Mustelidae. *Mammalia*, 33, 145–160.
- Long, C. A. & Frank, T. 1968. Morphometric variation and function in the baculum, with comments on correlation of parts. *Journal of Mammalogy*, 49, 32–43.
- Lüpold, S., McElligot, A. G. & Hosken, D. J. 2004. Bat genitalia: allometry, variation and good genes. *Biological Journal of the Linnean Society*, 83, 497–507.
- Malaivijitnond, S., Hamada, Y., Suryobroto, B. & Takenaka, O. 2007. Female long-tailed macaques with scrotum-like structure. *American Journal of Primatology*, 69, 721–735.
- Mayr, E. 1963. *Animal Species and Evolution*. Cambridge, Massachusetts: Harvard University Press.
- McPeck, M. A., Shen, L., Torrey, J. Z. & Farid, H. 2008. The tempo and mode of three-dimensional morphological evolution in male reproductive structures. *American Naturalist*, 171, E158–E178.
- Miller, E. H. 1991. Communication in pinnipeds, with special reference to non-acoustic signalling. In: *The Behaviour of Pinnipeds* (Ed. by D. Renouf), pp. 128–235. London, England: Chapman and Hall.
- Miller, E. H. 2009. Territorial behavior. In: *Encyclopedia of Marine Mammals*. Second ed. (Ed. by W. F. Perrin, B. Würsig & H. G. M. Thewissen), pp. 1156–1166. San Diego: Academic Press. (in press)
- Miller, E. H. & Burton, L. E. 2001. It's all relative: allometry and variation in the baculum (os penis) of the harp seal, *Pagophilus groenlandicus* (Carnivora: Phocidae). *Biological Journal of the Linnean Society*, 72, 345–355.
- Miller, E. H., Pitcher, K. W. & Loughlin, T. R. 2000. Bacular size, growth, and allometry in the largest extant otariid, the Steller sea lion (*Eumetopias jubatus*). *Journal of Mammalogy*, 81, 134–144.
- Mohr, E. 1963. Os penis und Os clitoridis der Pinnipedia. *Zeitschrift für Säugetierkunde*, 28, 19–37.
- Møller, A. P. 1995. Sexual selection in the barn swallow (*Hirundo rustica*). V. Geographic variation in ornament size. *Journal of Evolutionary Biology*, 8, 3–19.
- Muller, M. M. & Wrangham, R. 2002. Sexual mimicry in hyaenas. *Quarterly Review of Biology*, 77, 3–16.
- Murphy, W. J., Pringle, T. H., Crider, T. A., Springer, M. S. & Miller, W. 2007. Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Research*, 17, 413–421.
- Nunn, C. L. & Barton, R. A. 2001. Comparative methods for studying primate adaptation and allometry. *Evolutionary Anthropology*, 10, 81–98.
- O'Connor, M.P., Agosta, S. J., Hansen, F., Kemp, S. J., Sieg, A. E., McNair, J. N. & Dunham, A. E. 2007. Phylogeny, regression, and the allometry of physiological traits. *American Naturalist*, 170, 431–442.
- Paterson, H. E. H. 1993. *Evolution and the Recognition Concept of Species: Collected Writings* (Ed. by S. F. McEvey). Baltimore, Maryland: Johns Hopkins University Press.
- Patterson, B. D. 1983. Baculum-body size relationships as evidence for a selective continuum on bacular morphology. *Journal of Mammalogy*, 64, 496–499.
- Patterson, B. D. & Thaler, C. S. Jr. 1982. The mammalian baculum: hypotheses on the nature of bacular variability. *Journal of Mammalogy*, 63, 1–15.
- Perrin, W. F. & Mesnick, S. L. 2003. Sexual ecology of the spinner dolphin, *Stenella longirostris*: geographic variation in mating system. *Marine Mammal Science*, 19, 462–483.
- Pessõa, L. M. & dos Reis, S. F. 1992. Bacular variation in the subgenus *Trinomys*, subgenus *Proechimys* (Rodentia, Echimyidae). *Zeitschrift für Säugetierkunde*, 57, 100–102.
- Petter-Rousseaux, A. 1964. Reproductive physiology and behavior of the Lemuroidea. In: *Evolutionary and Genetic Biology of Primates*, vol. 2 (Ed. by J. Buettner-Janusch), pp. 91–132. New York: Academic Press.
- Pomiankowski, A. & Iwasa, Y. 1998. Runaway ornament diversity caused by Fisherian sexual selection. *Proceedings of the National Academy of Sciences of the U.S.A.* 95, 5106–5111.

- Prum, R. O. & Torres, R. H. 2004. Structural colouration of mammalian skin: convergent evolution of coherently scattering dermal collagen arrays. *Journal of Experimental Biology*, 207, 2157–2172.
- Ramm, S. A. 2007. Sexual selection and genital evolution in mammals: a phylogenetic analysis of baculum length. *American Naturalist*, 169, 360–369.
- Ramm, S. A., Parker, G. A. & Stockley, P. A. 2005. Sperm competition and the evolution of male reproductive anatomy in rodents. *Proceedings of Royal Society of London B* 272, 949–955.
- Raynaud, A. 1969. Mammelles. In: *Traité de zoologie: Anatomie, systématique, biologie*. Tome 16, Fascicule 6: Mammelles. Appareil génital gamétogénèse, fécondation, gestation (Ed. by P.-P. Grassé), pp. 1–853. Paris, France: Masson et Cie.
- Ritchie, M. G. 2007. Sexual selection and speciation. *Annual Review of Ecology and Systematics*, 38, 79–102.
- Roberts, W. E. 1988. Body and testis size in territorial and non-territorial northern fur seals (*Callorhinus ursinus*). *American Zoologist*, 28, 153A.
- Rommel, S. A., Pabst, D. A. & McLellan, W. A. 2007. Functional anatomy of the cetacean reproductive system, with comparisons to the domestic dog. In: *Reproductive Biology and Phylogeny of Cetacea: Whales, Dolphins and Porpoises* (Ed. By D. L. Miller), pp. 127–169. Enfield, New Hampshire: Science Publishers.
- Rönn, J., Katvala, M. & Arnqvist, G. 2007. Coevolution between harmful male genitalia and female resistance in seed beetles. *Proceedings of the National Academy of Sciences of the USA*, 104, 10921–10925.
- Scheffer, V. B. 1950. Growth of the testes and baculum in the fur seal, *Callorhinus ursinus*. *Journal of Mammalogy*, 31, 384–394.
- Seiffert, E. R. 2007. A new estimate of afrotherian phylogeny based on simultaneous analysis of genomic, morphological, and fossil evidence. *BMC Evolutionary Biology*, 7, 224.
- Setchell, B. P. & Breed, W. G. 2006. Anatomy, vasculature, and innervation of the male reproductive tract. In: *Knobil and Neill's Physiology of Reproduction*, vol. 1. Third edn. (Ed. by J. D. Neill), pp. 771–825. Amsterdam: Elsevier Academic Press.
- Simmons, M. N. & Jones, J. S. 2007. Male genital morphology and function: an evolutionary perspective. *Journal of Urology*, 177, 1625–1631.
- Simpson, G. G. 1945. The principles of classification and the classification of mammals. *Bulletin of the American Museum of Natural History*, 85, 1–350.
- Simpson, G. G. 1961. *Principles of Animal Taxonomy*. New York: Columbia University Press.
- Sloan, P. R. 1992. *Richard Owen's Hunterian Lectures at the Royal College of Physicians, May–June 1837*. Chicago: University of Chicago Press/London, England: British Museum of Natural History.
- Smith, J. D. & Madkour, G. 1980. Penial morphology and the question of chiropteran phylogeny. In: *Proceedings of the Fifth International Bat Research Conference* (Eds. D. E. Wilson & A. L. Gardner), pp. 347–365. Lubbock, Texas: Texas Tech Press.
- Springer, M. S. & Murphy, W. J. 2007a. Mammalian evolution and biomedicine: new views from phylogeny. *Biological Reviews* 82, 375–392.
- Springer, M. S. & Murphy, W. J. 2007b. Erratum. *Biological Reviews*, 82, 699.
- Springer, M. S., Burk-Herrick, A., Meredith, R., Eizirik, E., Teeling, E., O'Brien, S. J. & Murphy, W. J. 2007. The adequacy of morphology for reconstructing the early history of placental mammals. *Systematic Biology*, 56, 673–684.
- Stallmann, R. R. & Froehlich, J. W. 2000. Primate sexual swellings as coevolved signal systems. *Primates*, 41, 1–16.
- Steppan, S. J., Storz, B. L. & Hoffmann, R. S. 2004. Nuclear DNA phylogeny of the squirrels (Mammalia: Rodentia) and the evolution of arboreality from c-myc and RAG1. *Molecular Phylogenetics and Evolution*, 30, 703–719.
- Steppan, S. J., Adkins, R. M., Spinks, P. Q. and Hale, C. 2005. Multigene phylogeny of the Old World mice Murinae reveals distinct geographic lineages and the declining utility of mitochondrial genes compared to nuclear genes. *Molecular Phylogenetics and Evolution*, 37, 370–388.
- Stewardson, C. L., Bester, M. N. & Oosthuizen, W. H. 1998. Reproduction in the male Cape fur seal *Arctocephalus pusillus pusillus*: age at puberty and annual cycle of the testis. *Journal of Zoology*, 246, 63–74.

- Sullivan, R. M. & Petersen, K. E. 1988. Systematics of southwestern populations of least chipmunks (*Tamias minimus*) reexamined: a synthetic approach. *Occasional Papers of the Museum of Southwestern Biology*, 5, 1–27.
- Sutton, D. A. & Patterson, B. D. 2000. Geographic variation of the western chipmunks *Tamias senex* and *T. siskiyou*, with two new subspecies from California. *Journal of Mammalogy*, 81, 299–316.
- Symonds, M. R. E. 2005. Phylogeny and life histories of the 'Insectivora': controversies and consequences. *Biological Reviews*, 80, 93–128.
- Tinbergen, N. 1952. "Derived" activities; their causation, biological significance, origin, and emancipation during evolution. *Quarterly Review of Biology*, 27, 1–32.
- Voss, R. 1979. Male accessory glands and the evolution of copulatory plugs in rodents. *Occasional Papers of the Museum of Zoology, University of Michigan*, 689, 1–27.
- Wade, O. & Gilbert, P. T. 1940. The baculum of some Sciuridae and its significance in determining relationships. *Journal of Mammalogy*, 21, 52–63.
- West-Eberhard, M. J. 1983. Sexual selection, social competition, and speciation. *Quarterly Review of Biology*, 58, 155–183.
- Wickler, W. 1967. Socio-sexual signals and their intra-specific imitation among Primates. In: *Primate Ethology* (Ed. by D. Morris), pp. 69–147. London, England: Weidenfeld and Nicholson.
- Wickler, W. 1968. *Mimicry in Plants and Animals*. London, England: Weidenfeld and Nicholson.
- Wilkinson, G. S. & McCracken, G. F. 2003. Bats and balls: sexual selection and sperm competition in the Chiroptera. In: *Bat Ecology* (Ed. by T. H. Kunz & M. B. Fenton), pp. 128–155. Chicago, Illinois: University of Chicago Press.
- Wright, S. 1978. *Evolution and the Genetics of Populations, Volume 4: Variability Within and Among Natural Populations*. Chicago, Illinois: University of Chicago Press.
- Wyss, A. R. & Flynn, J. J. 1992. A phylogenetic analysis and definition of the Carnivora. In: *Mammal Phylogeny. Placentals* (Ed. by F. S. Szalay, M. J. Novacek & M. C. McKenna), pp. 32–52. New York: Springer-Verlag.
- Yablokov, A. V. 1974. *Variability of Mammals*. New Delhi, India: Amerind Publishing Company Pvt. Ltd.
- Zinner, D P., Nunn, C. L., van Schaik, C. P. & Kappeler, P. M. 2004. Sexual selection and exaggerated sexual swellings of female primates. In: *Sexual Selection in Primates: New and Comparative Perspectives* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 71–89. Cambridge, England: Cambridge University Press.