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REVIEW ARTICLE

Variation in Reproductive Behaviour within a Sex: Neural Systems and Endocrine Activation

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Abstract

Intrasexual variation in reproductive behaviour, morphology and physiology is taxonomically widespread in vertebrates, and is as biologically and ecologically significant as the differences between the sexes. In this review, we examine the diverse patterns of intrasexual variation in reproductive behaviours within vertebrates. By illustrating the genetic, cellular, hormonal and/or neural mechanisms underlying behavioural variation in a number of species, another level of complexity is added to studies of brain organization and function. Such information increases our understanding of the unique and conserved mechanisms underlying sex and individual differences in behaviour in vertebrates as a whole. Here, we show that intrasexual variation in behaviour may be discrete or continuous in nature. Moreover, this variation may be due to polymorphism at a single genetic locus or many loci, or may even be the result of phenotypic plasticity. Phenotypic plasticity simply refers to cases where a single genotype (or individual) can produce (or display) different phenotypes. Defined in this way, plasticity subsumes many different types of behavioural variation. For example, some behavioural phenotypes are established by environmental factors during early ontogeny, others are the result of developmental transitions from one phenotype early in life to another later in life, and still other strategies are facultative with different behaviours displayed in different social contexts.

The vertebrate brain is fundamentally bisexual. In other words, each individual has the neural substrates that regulate both female- and male-typical reproductive behaviours. This is best seen in hermaphroditic fish, where each individual displays a particular suite of 'female' behaviours when releasing eggs, but displays a different, complementary suite of 'male' behaviours when shedding sperm. The brain of higher vertebrates such as mammals is also initially bisexual or bipotential. In mammals, however, the regions of the brain that control reproductive and agonistic behaviour often differentiate such that the adult individual either displays female- or male-typical mating behaviour, but not both, during reproductive bouts. A great deal of research has focused on elucidating the neural and endocrine mechanisms that underlie such sexual dimorphisms in behaviour.

The foundation for decades of research on sex differences was laid down by Phoenix *et al.* (1) in their studies of sexual behaviour in guinea-pigs. These authors examined the behaviour of adult female guinea-pigs that had been exposed to testosterone propionate during embryonic development. In brief, they found that these females had a reduced capacity to display female-typical lordosis behaviour even when treated with doses of oestradiol benzoate and progesterone that facilitated this behaviour in normal females. In addition, they discovered that females exposed to testosterone propionate during embryonic development were more likely than normal females to display male-typical mounting behaviour when treated with testosterone in adulthood. In fact, females exposed to testosterone propionate during embryonic development behaved much like normal males when administered

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the same dose of the same hormones in adulthood. The authors concluded that 'androgenic substances received prenatally have an organizing action on the tissues mediating mating behaviour in the sense of altering permanently the responses females normally give as adults'.

Subsequent research has shown that, in general, a perinatal testosterone surge in male but not female mammals normally 'organizes' this sexually dimorphic responsiveness to hormone treatments in adulthood. More specifically, sex steroids regulate the differentiation of defined subregions of the hypothalamus by binding to their intracellular receptors, which act as transcription factors that alter gene expression. Important sites of action for sex steroids on reproductive behaviour, both during development and in adulthood, reside in the anterior hypothalamus-preoptic area continuum (AH-POA) and the ventromedial hypothalamus (VMH). These areas play integrative roles in the control of male- and female-typical sexual behaviours in all vertebrates examined to date (2). By and large, others have shown similar hormone-dependent mechanisms of neural and behavioural differentiation in amphibians (3), birds (4) and reptiles (5).

Although this body of work on sex differences has allowed a fundamental understanding of hormone–brain–behaviour relationships, it neglects an equally important concern, namely individual differences in behaviour within each sex. Almost 25 years ago, reports began to appear of species in which males exhibited categorical variation in morphology, physiology and behaviour. These differences were usually characterized as alternative mating strategies consisting of a colourful, territorial male phenotype contrasting with another, less frequent male phenotype that was more similar to juvenile animals or even females. Males with these alternative phenotypes usually obtain matings with females by deception or confusion of territorial males.

Moore (6) suggested that discrete differences within a sex could be understood within the context of the organization–activation theory for sex differences. In particular, he proposed that there is a fundamental distinction between systems with fixed or plastic alternative male phenotypes. His definition of a fixed system is one 'in which individual males assume one phenotype for their adult lives'. By contrast, his definition of a plastic system is one 'in which individual males can change phenotypes at least once'. He further proposed that organizational influences of hormones will be most important in the development of fixed, alternative male phenotypes and that activational influences of hormones will be most important in the regulation of plastic, alternative male phenotypes. Although this theoretical framework, called the 'relative plasticity hypothesis', is intuitively appealing and has been of some heuristic use, it fails to account for the complexity of intrasexual variation in behaviour in two important ways.

First, a broader perspective is needed to encompass the full gamut of intrasexual variation in behaviour. Behavioural variation within a sex actually ranges from one extreme in which continuous variation occurs without distinct phenotypes to another extreme with discrete alternative phenotypes and little or no overlap in phenotype between groups (Fig. 1). In some cases, the pattern of behavioural variation may reflect underlying genetic mechanisms. For example, there is a

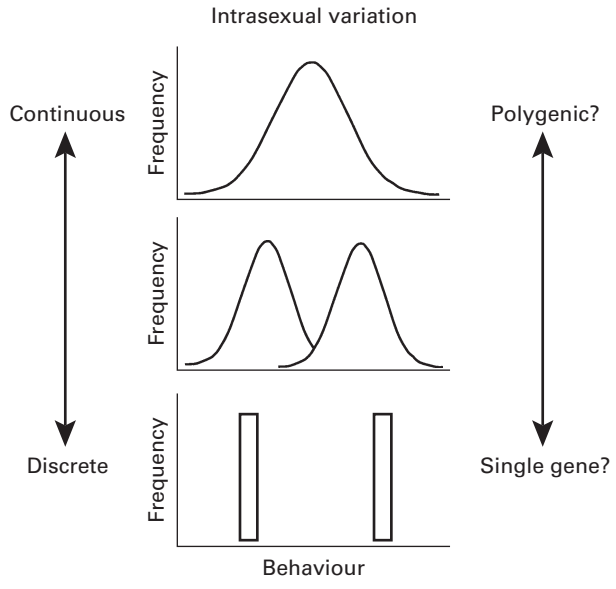

FIG. 1. Theoretical frequency distributions for behavioural variation within a sex. Behaviours range from one extreme in which continuous variation occurs without distinct phenotypes to another extreme with discrete alternative phenotypes. These patterns of behavioural variation may reflect underlying genetic mechanisms: whereas many genes may influence traits that display continuous variation, traits with discrete phenotypes may be controlled by a single locus.

distinction in population genetics between traits that display continuous variation and are controlled by many genes (i.e. polygenic or quantitative traits) versus traits with discrete phenotypes controlled by a single locus (i.e. Mendelian traits) (Fig. 1). Thus, although discrete phenotypes are often easier to study, a focus on such systems may lead to a bias in our understanding of mechanisms underlying individual variation in reproductive behaviour.

A second, but more significant, problem is Moore's basic formulation of the 'relative plasticity hypothesis', which blends the usual concept of phenotypic plasticity with the organizational and activational effects of steroid hormones (Fig. 2A). In particular, his unorthodox definition of fixed versus plastic phenotypes does not make a distinction between alternative phenotypes that are a result of a genetic polymorphism versus alternative phenotypes that are plastic and sensitive to environmental influences early in development but not in adulthood (i.e. polyphenisms). Alternative phenotypes are only considered plastic if individual males change phenotypes at least once in adulthood. However, the classic definition of phenotypic plasticity is broader and does not dictate the developmental stage when plasticity is evident or the physiological mechanism underlying plasticity. Phenotypic plasticity simply refers to cases where a single genotype can produce different phenotypes, often in response to an environmental variable. Defined in this way, plasticity itself can be considered a strategy that subsumes many different phenomena. For example, some plastic phenotypes are established by environmental factors during early ontogeny (e.g. polyphenisms), others are the result of developmental transitions from one strategy early in life to

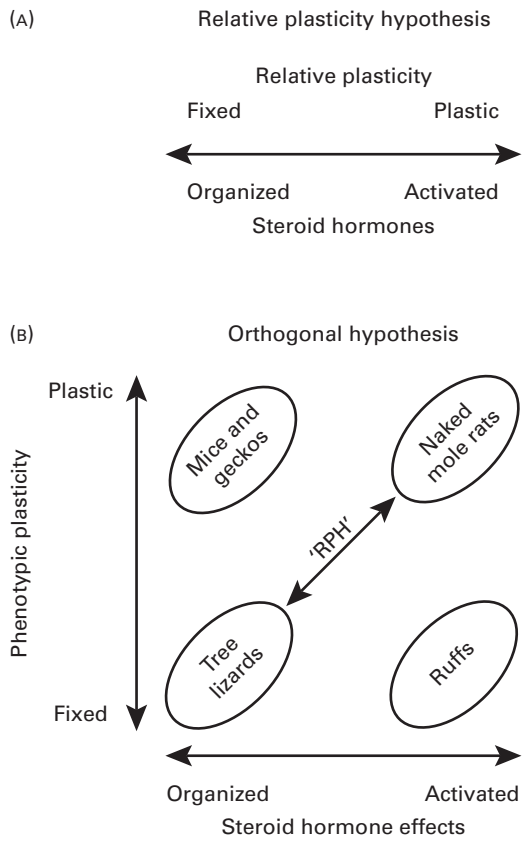

FIG. 2. (A) Schematic representation of the 'relative plasticity hypothesis' for the hormonal basis of intrasexual variation in reproductive behaviour. (B) Schematic representation of the 'orthogonal hypothesis' for the hormonal basis of intrasexual variation in reproductive behaviour. The 'relative plasticity hypothesis' is a subset of the possible hormonal mechanisms underlying variation in reproductive behaviour. Species that conform to the 'relative plasticity hypothesis', as well as those that do not, are indicated.

another later in life (e.g. metamorphosis), and still other strategies are facultative with different phenotypes displayed in different social contexts (e.g. dominance–subordinance relationships).

We therefore submit that the plasticity of a behavioural trait is orthogonal to the organizational and activational effects of steroid hormones on that trait (Fig. 2B). In other words, species may have phenotypes that are controlled by hormonal mechanisms 'off the diagonal' that lies between 'fixed traits' and that are organized by steroids early in life and 'plastic traits' that are activated by steroids later in life. This diagonal is the basic formulation of the 'relative plasticity hypothesis' (Fig. 2B). In this review, we provide examples of species (i.e. mice and geckos) where sex steroids play a role in organizing phenotypes that are plastic during early development and other examples (i.e. birds called ruffs) where sex steroids activate a genetic polymorphism for alternative phenotypes in adulthood. In addition, the development of intrasexual variation in behaviour may be via mechanisms that are independent of steroid hormones. A broader perspective of phenotypic plasticity will lead to a more complete understanding of the mechanisms underlying intrasexual variation in reproductive behaviour.

In summary, intrasexual variation may be continuous or discrete in nature. Moreover, this variation may be the result of genetic polymorphism or phenotypic plasticity, both of which can be expressed at any developmental stage. It is now evident that intrasexual variation in behaviour is taxonomically widespread in vertebrates and is as biologically and ecologically significant as the differences between the sexes. For example, intrasexual variation in reproductive behaviour has obvious implications for mating systems, thereby influencing patterns of gene flow and other evolutionary processes. Such consequences are beyond the scope of this article. Here, we review what is known and unknown about the genetic, cellular, hormonal and/or neural mechanisms underlying variation in behaviour within the sexes. By using representatives from all the major vertebrate classes and examining both continuous and discrete variation, we hope to illustrate the tremendous potential for further research on intrasexual variation in reproductive behaviour. Our discussion of various model systems is inevitably uneven because some species have been examined at the single cell, electrophysiological level and others primarily at a gross behavioural level. In discussing the available data for such species, we can identify gaps in our knowledge and suggest experiments that will fill in these holes. Ultimately, information on intrasexual variation in reproductive behaviour will elucidate the evolution of unique and shared aspects of neuroendocrine development and function in all vertebrates.

Fish

The manner in which fish reproduce is remarkably variable. For example, sequentially hermaphroditic species reproduce first as males then switch permanently to female status while other species display the converse pattern. By contrast, simultaneously hermaphroditic species alternate between donating sperm and eggs without permanent gonadal differentiation. The brain and behaviour are clearly not differentiated in the latter species, which facultatively switch between 'male' and 'female' behaviours. The physiological and neural mechanisms responsible for this behavioural plasticity have not been elucidated completely, but do appear to involve discrete neural pathways that control sex-typical colour patterns and gamete release (7). There are also changes in expression of gonadotropin releasing hormone (GnRH) and arginine vasotocin (AVT) correlated with the changes in reproductive roles described above (8). By contrast to the sexual plasticity seen in hermaphroditic species, other species of fish are developmentally committed to reproduce as only one sex. Nevertheless, those species with separate males and females commonly display intrasexual variation in behaviour.

One of the most frequently observed types of variation in reproductive behaviour in all vertebrates, including fish, occurs when males display one of two distinct behavioural phenotypes: a guarding tactic or a sneaker strategy (9). In this section, we will discuss two species that display discrete alternative phenotypes. Whereas the genetic basis of alternative phenotypes is known in swordtails (*Xiphophorus maculatus*), the neuroendocrine mechanisms underlying

alternative behavioural strategies are best characterized in the plainfin midshipman (*Porichthys notatus*). Type I male plainfin midshipman build nests, produce courtship vocalizations called 'hums' to attract females, and are parental, whereas the type II males manifest none of these behaviours, practicing a satellite or sneaker strategy to reproduce (10).

Type I and II males follow distinct ontogenetic trajectories and do not switch behavioural tactics. Consequently, these males differ in body size, have dimorphic vocal circuitry and sonic muscle morphology, and differ in the number and size of GnRH-containing cells with type I males showing greater development in all these traits (11–16). Type I males also have higher levels of 11-ketotestosterone (the more potent androgen in teleosts) and lower levels of testosterone than type II males. This is the case even though type II males reach sexual maturity earlier than type I males (17). Taken together, these findings suggest that type II males ostensibly retain juvenile or female characteristics despite attaining sexual maturity (i.e. these males are paedomorphic).

This pattern of intra- and intersexual differentiation was illustrated elegantly in a recent study of neuropeptide effects on grunt vocalizations in the plainfin midshipman (18). Although agonistic grunts are produced by both types of males and by females, there are quantitative differences in the behaviour among males and females. Moreover, this behaviour is displayed in different social situations: Type I males emit long trains of grunts during defense of their nests whereas type II males and females emit short grunts in nonreproductive contexts. Interestingly, AVT and isotocin have differential effects on these vocalizations when administered to the AH-POA (Fig. 3). In type I males, application of an electrical stimulus to the tuberal region of the AH-POA induces grunts whereas application of AVT inhibits electrically stimulated grunts. By contrast, isotocin had no effect on electrically stimulated grunts in type I males. Females display just the opposite pattern of neuropeptide responsiveness. When applied to the AH-POA of females, AVT has no behavioural effect whereas isotocin inhibits electrically stimulated grunts. Type II males display a pattern of sensitivity to neuropeptides that is very similar to that found in females. These experiments clearly demonstrate the neuroendocrine basis of an alternative reproductive behaviour in the male plainfin midshipman and show that one of these alternatives essentially mimics the female phenotype.

The genetic basis of male phenotypes in the plainfin midshipman is still unknown, but another fish species, a swordtail, has a defined genetic polymorphism where males of different size classes display different patterns of behaviour (19, 20). In the swordtail, a locus on the Y chromosome determines whether a male matures early at a small size and chases females or matures later at a large size and courts females. The mechanism that translates this genetic polymorphism into a behavioural and morphological polymorphism appears to involve differential development of GnRH-containing neurones within the brain (21, 22).

In early maturing male swordtails, immunoreactive GnRH-containing first appear in the nucleus olfactoretinalis at 5 weeks of age. By contrast, these neurones appear at 11 weeks of age in late-maturing males. Once developed, however, there are no differences in the numbers or size of

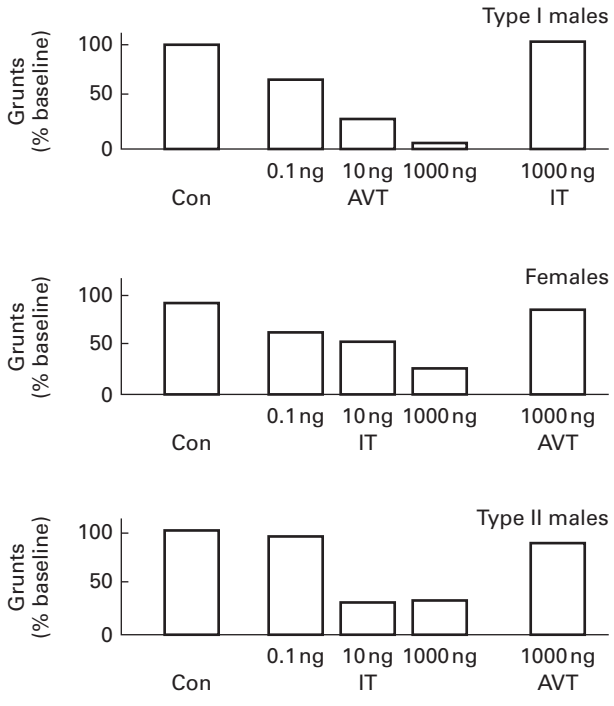

FIG. 3. Effects of arginine vasotocin (AVT) and isotocin (IT) on electrically stimulated grunts in type I male, female, and type II male plainfin midshipman as a percentage of the total duration of grunts elicited in control animals (Con). After (18).

the cells expressing GnRH within the nucleus olfactoretinalis. However, early maturing males have more immunoreactive GnRH neurones in the nucleus preopticus periventricularis and nucleus lateralis tuberis than do late-maturing males. The same difference occurs in the pituitary where immunoreactive GnRH cells are more abundant in early maturing males. Interestingly, exogenous testosterone and 11-ketotestosterone influence the synthesis and/or release of GnRH in both genotypes before they reach sexual maturity. Nevertheless, these two androgens act upon different GnRH containing regions of the brain and have distinct effects on the rate of sexual maturation (23). It remains to be determined if there are differences in endogenous levels of testosterone and 11-ketotestosterone between the early and late-maturing genotypes that might explain differences in the GnRH system and hypothalamus as well as differences in developmental rate.

Swordtails and plainfin midshipman are just two of many fish species that display alternative male phenotypes. However, it is unclear if mechanisms similar to those found in these species underlie discrete phenotypes in other species. A particularly promising area for future work includes cloning of the gene on the Y chromosome in swordtails. After such a gene is identified and characterized at the molecular level, it would be possible to determine how one locus with alternative alleles has pleiotropic effects on the development of GnRH-containing neurones, behaviour, and morphology. In plainfin midshipman, experiments could be directed at determining if alternative male tactics are due to a genetic polymorphism. If so, it would also be enlightening to identify

the gene and clone the locus involved. Another fruitful avenue would be to determine if the different ratios of 11-ketotestosterone to testosterone cause any of the phenotypic differences between type I and type II male plainfin midshipman.

Amphibians

Unlike fish, amphibians display relative uniformity in their basic mode of reproduction. All frogs and urodeles (i.e. salamanders and newts) studied to date have separate males and females. As in mammals, gonadal sex is determined by sex chromosomes, although exposure to high embryonic temperatures can reverse gonadal sex in some species (24, 25). In addition, the pattern of sexual differentiation of non-gonadal tissues, including the brain and vocalization behaviour, generally appears to follow the model outlined for mammals (26, 27). However, the entire testis, rather than just androgens, is required to fully masculinize the song system in the South African clawed frog (3). This suggests that the testes secrete additional factors required for sexual differentiation of the brain in this species.

As in fish, there is intrasexual variation in reproductive behaviour within male frogs. Strawberry poison-dart frogs (*Dendrobates pumillo*), for example, display skin colour and pattern variation among populations in Panama (28). By contrast, other sympatric species of poison-dart frogs exhibit little colour or pattern variation among populations. Interestingly, females provide parental care in the polymorphic species whereas males are parental in the monomorphic species. Although it has been suggested that sexual selection by females for alternative male types is associated with maternal care, it is unclear whether there are any behavioural or other phenotypic differences associated with variation in skin pigment. Similarly, nothing is known about the genetic or physiological basis of skin colour and pattern variation or parental behaviour. In any case, there is the potential for sexual selection as male frogs, in general, form large groups dubbed choruses during the mating season and make advertisement calls to attract females. In the remainder of this section, we will focus on intrasexual variation in calling behaviour.

In frogs, where the neuroendocrine basis of vocalization has been studied in some detail, individual males may display a calling strategy or a satellite strategy in which they lie in wait and attempt to mate with females as they approach calling males (29, 30). In contrast to the fixed alternative behaviours displayed by plainfin midshipman, these behavioural tactics are facultative: males can switch strategies in different social contexts (30). Males appear to adopt the satellite strategy when adjacent males are using low sound frequencies, which is generally indicative of larger body size. Possible neuroendocrine mechanisms underlying such facultative changes in behaviour likely involve synthesis, release, and sensitivity to AVT.

Sexual dimorphisms in the vasotocin system are evident in adult bullfrogs (*Rana catesbeiana*) but not in juveniles (31–33). Androgens and oestrogens differentially regulate the expression of AVT and/or its receptor in the brain of frogs and newts (34–36). Moreover, AVT has different effects on the behaviour of adult males and females. In female bullfrogs, AVT stimulates phonotaxis or movement toward a calling male (37) but, in males, stimulates advertisement calls. The latter effect is also seen in males of some other frog species (37, 38). For example, vocalization behaviour under natural conditions is correlated with AVT levels in the forebrain of male cricket frogs (*Acris crepitans*) (39). Satellite males have significantly greater AVT-immunoreactive staining within the nucleus accumbens than calling males (Fig. 4). The authors hypothesized that calling males are releasing AVT from the nucleus accumbens and therefore have depleted intracellular stores of AVT when compared to silent satellite males. In accordance with this hypothesis, injection of AVT stimulates males to begin calling sooner during a simulated agonistic

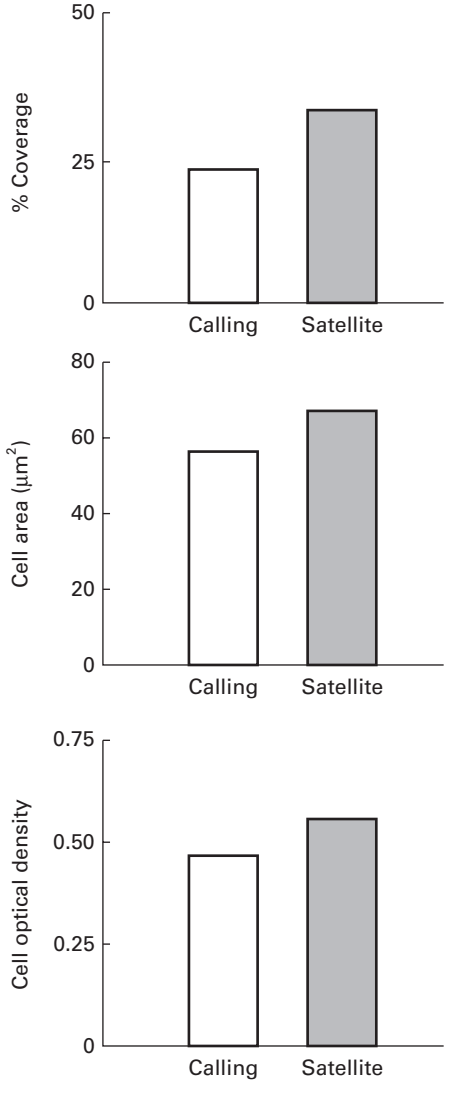

FIG. 4. Differences in arginine vasotocin (AVT) immunoreactive cells in the nucleus accumbens between calling and satellite male cricket frogs. Satellite males had more AVT immunoreactivity than calling males as measured by the area covered by stained cells and fibres, the average size of AVT immunoreactive cells and the optical density of AVT immunoreactive cells in the nucleus accumbens. After (39).

encounter and to call more often during and after the encounter (40). Consequently, if AVT plays a key role in the motivational aspects of advertisement calling, it should be possible to place cannulae into the nucleus accumbens, alter extra-cellular AVT levels, and manipulate the production of advertisement calls in male cricket frogs.

Some tantalizing data shed light on the mechanism(s) that may influence the decision to call or to adopt a satellite strategy. Stress, similar to proximity to a larger male, inhibits reproductive behaviour in male frogs. For example, advertisement calls cease when grey treefrog males (*Hyla versicolor*) are subjected to prolonged captivity or saline injections (38). In contrast, AVT injections either restore or maintain advertisement vocalizations in the face of such stressors. The inhibitory effects of stress may be mediated via the hypothalamic-pituitary-adrenal axis, glucocorticoids, and the GABAergic system. In the rough-skinned newt (*Taricha granulosa*), confinement stress, corticosterone, or GABA agonists suppress male sex behaviour (41). The inhibitory effects of these compounds are blocked in turn by pretreatment with an inhibitor of GABA synthesis. A similar neuroendocrine mechanism may be responsible for the inhibition of vocalization in treefrogs that switch from a calling to a satellite strategy because corticosterone inhibits calling in AVT-injected male green treefrogs (*Hyla cinerea*), but only at a relatively high dose (42). Isolated males of this species have higher circulating levels of androgens and corticosterone when exposed to a recording of a mating chorus than do control males exposed to an array of tones or to no sound at all (43). However, elevated levels of corticosterone in the latter study did not appear to inhibit calling behaviour. Consequently, it remains unclear what role endogenous glucocorticoids play in the inhibition of advertisement calling and the adoption of a satellite strategy.

In any event, the facultative display of different behavioural strategies in male frogs presents an excellent model system for studying neuroendocrine mechanisms underlying behavioural plasticity and alternative reproductive tactics. It is important to note that AVT modulates the likelihood of vocalization by both the male plainfin midshipman and male frogs. However, the pattern of effects differs because AVT increases (or maintains) calling in frogs but inhibits calling in the plainfin midshipman. A potentially confounding factor in this comparison is that the vocalizations examined are of different types. Whereas advertisement calls were studied in frogs, agonistic calls were examined in the plainfin midshipman. Further studies are required to clarify the role of AVT in courtship versus agonistic behaviours in a single species of frog. In addition, frogs that have been studied so far display facultative behavioural strategies. It will be critical to examine the mechanisms underlying calling behaviour in species like strawberry poison-dart frogs that may display fixed alternative strategies.

Reptiles

This diverse group of vertebrates exhibits variation in modes of sex determination. Snakes have genotypic sex determination with heterogametic females (i.e. ZW sex chromosomes) and homogametic males (i.e. ZZ sex chromosomes). All crocodilians have temperature-dependent sex determination where incubation temperature during a critical period of embryonic development determines gonadal sex (44). Many turtles and some lizards also have temperature-dependent sex determination, but the rest have genotypic sex determination (45, 46). Alternative reproductive strategies occur frequently in lizards, which are more amenable than turtles and crocodilians to studies of the neural and hormonal bases of behaviour. In this section, we discuss data on three lizard species that display patterns of behavioural variation that differ from those described so far. We will describe two species that have discrete alternative phenotypes that appear to result from a genetic polymorphism, like swordtails. Unlike the fish, however, one morph displays a fixed, territorial strategy and the other morph a plastic phenotype that changes either during development or in response to environmental factors. The third species provides a classic example of phenotypic plasticity, where incubation temperature during embryonic development alters a suite of traits.

An interesting set of strategies is observed in side-blotched lizards (*Uta stansburiana*). Males in this species come in three morphs that display different patterns of reproductive behaviours. Orange-throated and blue-throated males are territorial, but yellow-throated males are nomads that do not defend a territory (47). Although orange- and blue-throated males both defend territories, orange-throated males are very aggressive and maintain larger territories with more resident females than do blue-throated males. Consequently, orange-throated males have the opportunity to mate with more females than blue-throated males (48). In contrast to orange-throated males, blue-throated males closely guard females on their territory. Nomadic yellow-throated males are able to obtain furtive copulations with females on the large territories of the highly polygynous, orange-throated males but have lower success on the territories of blue-throated males that guard their females (48). Data discussed below suggest that the yellow-throated males actually develop into blue-throated males, thus representing a single plastic morph that changes phenotype during adulthood. Multiple reproductive tactics in this species appear to be an evolutionary stable strategy in which there are cyclical changes in the frequency of the three male morphs that depend upon which type of male is the most common in the population at a given time (47). For example, the orange strategy beats the blue strategy if blue-throated males are common, the blue strategy beats the yellow strategy if yellow-throated males are common, and the yellow strategy beats the orange strategy if orange-throated males are common.

The hormonal mechanism underlying these alternative reproductive strategies has recently been investigated (49). Orange-throated males have higher levels of testosterone, endurance and activity levels than blue- or yellow-throated males, which goes along with their larger territory size. Interestingly, testosterone treatment of blue- and yellow-throated males increased their endurance, activity levels and territory size to the levels seen in unmanipulated orange-throated males. In addition, testosterone levels increased naturally during the reproductive season in some yellow-throated males. In conjunction with the change in plasma testosterone levels, these yellow-throated males

developed blue throats and changed to a territorial strategy. These results suggest that testosterone plays a central role in generating alternative reproductive strategies in this species. Although there appears to be plasticity in the display of the yellow and blue morphs, the developmental basis of the difference between the yellow-blue morph and the orange, super territorial morph remains unclear. However, yellow-blue morphs have never been observed to take on the orange morphology or behavioural strategy, which is consistent with a high heritability for the alternative male phenotypes (48). It will be interesting to test the hypothesis that differences in testosterone levels during early ontogeny regulate differentiation of males into the yellow-blue-throated morph versus the orange-throated morph.

Such organizational actions of androgens have been demonstrated in the tree lizard (*Urosaurus ornatus*), another species with alternative male strategies (50–52). Orange males have an orange dewlap (throat), are nonterritorial and are larger than orange-blue males that are territorial and have a blue patch on their orange dewlap. Whereas castration of male tree lizards early in development results in a high frequency of the orange, nonterritorial morph, testosterone treatment produces more orange-blue, territorial males. Although these initial results suggested that testosterone plays a key role in the development of alternative phenotypes, subsequent work implicates progesterone as the physiological signal that regulates morphological and behavioural differentiation in the tree lizard. There is a perinatal surge in progesterone levels in males that develop the orange-blue, territorial phenotype, but not in males that develop the orange, nonterritorial phenotype (53). In addition, treatment with exogenous progesterone during early development mimics the effect of (or is more effective than) testosterone on development of the orange-blue, territorial phenotype. Interestingly, orange-blue males with a territorial strategy are less sensitive to the inhibitory effects of stress and glucocorticoids on reproduction that are orange, nonterritorial males (54, 55). Moreover, orange, nonterritorial males appear to conditionally switch tactics, displaying sedentary satellite behaviour when environmental conditions are relatively benign and a nomadic lifestyle when environmental conditions are harsh (53). Evidence suggests that differences in sensitivity to glucocorticoids between territorial males and satellite-nomadic males may be mediated by differences in circulating levels of a glucocorticoid binding globulin, which is found at a higher level in territorial males (55). Consequently, the glucocorticoid binding globulin could absorb glucocoticoids and make orange-blue, territorial males less sensitive to the effects of glucocoticoids and stress.

Phenotypic plasticity is responsible for intrasexual variation in behaviour in the leopard gecko (*Eublepharis macularius*). Rather than a genotype-based difference in reproductive strategies, variation in ambient temperature during embryogenesis induces the development of different behavioural repertoires and physiology in the leopard gecko (56). The key features of leopard gecko biology relevant here are that embryonic incubation temperature determines gonadal sex and that both incubation temperature and gonadal sex affect circulating levels of sex steroid hormones, sexual and aggressive behaviour, and the size and metabolic capacity of brain nuclei in the adult animal. The hormonal mechanisms underlying sex differences in behaviour have been examined and appear to follow the general paradigm found in mammals (57, 58). In brief, females ovariectomized in adulthood and treated with oestradiol display female-typical receptive behaviour whereas castrated males are unreceptive even when treated with the same level of oestradiol and mounted by the same stimulus males. Conversely, ovariectomized females display very little male-typical sexual and aggressive behaviour even when treated with levels of androgens that activate these behaviours in males. These sex differences in hormonal responsiveness in adulthood are most likely organized by sex differences in steroid levels during ontogeny because male leopard geckos have higher levels of dihydrotestosterone and testosterone than females throughout postnatal development (59).

Although intrasexual variation in reproductive behaviour occurs in both sexes in the leopard gecko, we will focus on temperature-induced differences in males. Incubation of leopard gecko eggs at 26 °C produces only females, 30 °C produces a female-biased sex ratio (approximately 30% males), 32.5 °C produces a male-biased sex ratio (approximately 70% males) and 34 °C again produces virtually all females. Interestingly, males from the female-biased (i.e. 30 °C) incubation temperature are more sexually active and less aggressive towards females than males from the male-biased (i.e. 32.5 °C) temperature (60). Incubation temperature also influences endocrine physiology such that oestrogen levels are higher and testosterone levels are lower in adult males from the female-biased versus adult males from the male-biased temperature (61, 62). Nevertheless, incubation temperature-induced differences in certain behaviours do not depend upon differences in circulating hormone levels in adulthood. Males from the male-biased incubation temperature scent mark more (a territorial behaviour) than do males from the female-biased temperature even when both types of males are treated with the same levels of testosterone or dihydrotestosterone (Fig. 5). Conversely, and across the same hormone treatments, males from the female-biased incubation temperature mount stimulus females more than do males from the male-biased incubation temperature (Fig. 5). These results suggest that incubation temperature during embryonic development has a permanent effect on the organization of the male leopard gecko brain.

In accordance with this hypothesis, the effects of incubation temperature on metabolic capacity and the size of certain forebrain nuclei correlate with the sexual and agonistic behaviour displayed by adult male and female geckos that come from different incubation temperatures (62, 63). For example, males from the female-biased temperature (i.e. more sexually active males) have greater metabolic capacity in the POA, dorsoventricular ridge and torus semicircularis than their counterparts from the male-biased temperature (i.e. less sexually active males). Such an incubation temperature-induced difference in metabolic capacity in the POA would be expected if there is a functional relationship between neuronal activity in this brain region and male sexual behaviour. In contrast, the size of the POA is significantly larger in males from the male-biased temperature than in males from the female-biased temperature (63). Incubation

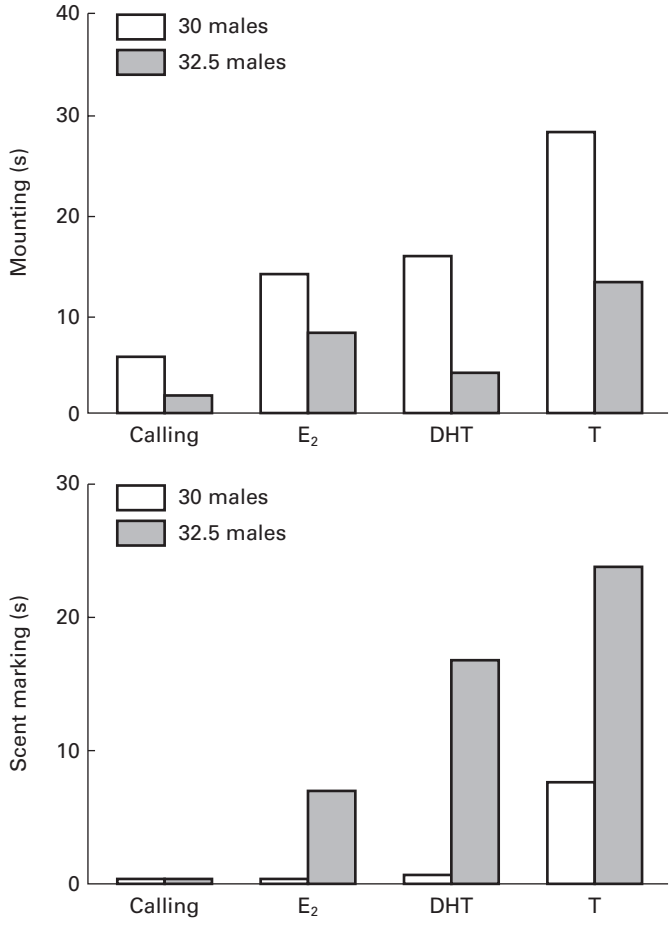

FIG. 5. Effects of embryonic incubation temperature and adult hormone treatment on mounting (upper panel) behaviour and scent marking (lower panel) of castrated male leopard geckos. After (57). Castrated males received a silastic implant containing cholesterol, 17β-oestradiol (E_2), dihydrotestosterone (DHT) or testosterone (T).

temperature also influences metabolic capacity in other behaviourally relevant nuclei. Males from the male-biased temperature have higher metabolic capacity than do males from the female-biased temperature in the septum, anterior hypothalamus and nucleus sphericus, all areas involved in the regulation of agonistic behaviour in other vertebrate species. In addition, incubation temperature affects covariance patterns in metabolic capacity among these and other nuclei (64), suggesting that temperature-induced correlations in metabolic capacity among critical nuclei might reflect differences in functional connectivity.

Although embryonic incubation temperature has pleiotropic effects on sexual and agonistic behaviour, as well as neural phenotype, in the male leopard gecko, it is not known how temperature exerts its effects on the brain. Various studies suggest that temperature determines gonadal sex in reptiles by influencing sex steroid metabolism during embryonic development (65, 66). Because sex determination is a threshold trait (i.e. sex ratio varies but there are no hermaphrodites produced), individuals with oestrogen levels below a certain threshold develop as males and individuals with oestrogen levels above the threshold develop as females. This model predicts that individuals of the same sex from different incubation temperatures are exposed to different hormonal milieus during embryonic development. Consequently, temperature-induced variation in hormone production during early development could affect numerous physiological and behavioural traits later in life.

Alternatively, incubation temperature might have effects on leopard gecko physiology and behaviour that are not mediated by sex steroids. Female leopard geckos from oestrogen-treated eggs incubated at the male-biased temperature (32.5 °C) do not differ in growth rates or aggressiveness from unmanipulated females from the same incubation temperature (61). Experiments on the common snapping turtle, another reptile with temperature-dependent sex determination, indicate that sex steroid hormones do not mediate embryonic temperature effects on postnatal physiology and behaviour (67–71). In these studies, snapping turtle eggs were incubated at two temperatures that normally produce only males and a third that produces a female-biased sex ratio. Eggs were treated during the thermosensitive period with oestrogen, a potent aromatase inhibitor, a vehicle control, or were not treated at all. In agreement with other studies, gonadal sex was reversed by hormonal manipulations: oestrogen produced females at male-producing temperatures and the aromatase inhibitor produced males at the female-producing temperature. By contrast, neither hormone treatment nor gonadal sex influenced hatchling size, residual energy stores, posthatching growth rate, or thermoregulatory behaviour. Nevertheless, embryonic temperature had very strong effects on these traits. These experiments indicate that temperature can influence neuroendocrine and behavioural differentiation in reptiles with temperature-dependent sex determination via mechanisms that do not involve sex steroids.

In summary, side-blotched lizards and tree lizards have alternative male phenotypes that are generally similar to one another. One morph in both species displays a fixed, territorial strategy. The other morph exhibits a plastic phenotype that changes during development in the side-blotched lizard and facultatively in response to environmental factors in the tree lizard. If feasible, future studies could determine if fixed versus plastic morphs result from a genetic polymorphism in both species. Other studies could examine the neural differences or mechanisms underlying alternative phenotypes in these species. By contrast, leopard geckos provide a classic example of phenotypic plasticity. Considering the 'organizational' effect of incubation temperature on the metabolic capacity of the brain and behaviour, future work in this species should focus on characterizing incubation temperature-induced differences in hormone levels and gene expression in the brain during embryonic development. Differential display or subtractive hybridization techniques would be extremely useful for such studies (72).

Birds

Birds have genotypic sex determination with heterogametic females and homogametic males. Sex steroids have a primary effect on sexual differentiation and activation of sexual and

agonistic behaviour in birds, much as they do in most other vertebrates. Female Japanese quail (*Coturnix japonica*) are 'demasculinized' by elevated levels of oestradiol during the perinatal period. Specifically, they lose the ability to display male-typical mounting behaviour when treated with testosterone (or oestrogens) as adults (73, 74). In contrast, male Japanese quail retain the capacity to display female-typical sexual behaviour when treated with oestrogens in adulthood. The finding that sex steroid hormones regulate sexual differentiation of the brain and behaviour in birds sets the stage for intrasexual variation in reproductive behaviour due to subtle variation in exposure to sex steroids during early ontogeny. In fact, steroid hormones in the egg yolk mediate maternal effects on offspring phenotype in a number of species. We briefly discuss the effects of these maternal steroids on intrasexual variation in growth, morphology, and behaviour. We then switch gears and describe a species in which discrete male phenotypes result from activation of a genetic polymorphism in adulthood. Sex steroid hormones do not appear to play any role in the organization of alternative phenotypes in the latter species.

Recent work has shown that maternal steroid hormones deposited in the yolk of bird eggs influence subsequent development of the offspring. In canaries (*Serinus canaria*), the laying order of eggs in a clutch correlates with testosterone levels in the yolk, such that the last egg laid has a higher concentration of testosterone than the first egg laid. Testosterone levels, in turn, correlate with postnatal differences in begging behaviour, growth rate and aggressive behaviour among hatchling canaries (75, 76). A similar increase in testosterone levels with laying order occurs in red-winged blackbirds (*Agelaius phoeniceus*) (77). Experimental blockage of androgen action or supplementation of yolk androgens in this species suggest that maternally derived testosterone enhances development of the hatching muscle of offspring. It is interesting to note that the laying order of eggs has a strong, sex-specific effect on growth in house finches (*Carpodacus mexicanus*) (78). Growth rate decreases with hatching order in males but increases with hatching order in females in a Montana population of house finches. The opposite pattern was observed in a population from Alabama: growth rate decreases with hatching order in females but is greatest in males in the middle of the brood. Sex ratio also varies with laying order in these populations. First laid eggs produce male-biased sex ratios and last laid eggs produce female-biased ratios in Montana. By contrast, first laid eggs produce female-biased sex ratios and last laid eggs result in male-biased ratios in Alabama. This association between laying order, hatchling sex ratio and sex-specific effects on growth appear to reduce juvenile mortality rates in an adaptive manner. The mechanisms underlying laying order effects in the house finch are still unknown, but may involve maternal deposition of sex steroids in the yolk. Whether variation in growth, morphology and behaviour of hatchling birds carries over into adulthood and influences reproductive behaviour is currently unknown, but certainly deserves further study.

A clear set of alternative reproductive tactics is evident in male ruffs, a sandpiper found in Northern Europe and Russia. In this species, some males establish territories on breeding grounds, defend their territory against other males and remain on their territory for extended periods. Satellite males, on the other hand, reside on these territories in transient coalitions with the territory-holding males: satellites are highly mobile and move frequently among territories held by different males. Overall, it appears that both types of males benefit from these temporary coalitions because females prefer to visit and mate on territories co-occupied by a territorial male and a satellite male (79, 80; David Lank, personal communication). In fact, territorial males try to attract satellites to their territories. This coalition is not without conflict, however, as territorial males try to prevent satellites from mating with visiting females. Although territorial males lose some mating opportunities to satellites on their territory, they have a greater chance of mating with females than do males whose territories lack a satellite. From the satellite's point of view, it may be best to associate with an attractive territorial male, which may explain their frequent movement among territories. In conjunction with these behavioural observations, there is genetic evidence that female ruffs are highly polyandrous and produce offspring from both territorial and satellite males within the same clutch (81). This behavioural dimorphism is the result of a single locus, autosomal polymorphism that determines whether a male becomes a territorial or a satellite male (82). Interestingly, there are also differences in plumage traits between territorial and satellite males, with satellites tending to have lighter colouration (83).

Administration of androgens to adult females will cause them to express a full suite of male-typical behaviours and develop male display feathers and facial wattles (84). The alternative behaviours displayed by these females corresponded to the behavioural and morphological phenotypes of their brothers and half-brothers, as expected based on the autosomal inheritance of this trait. However, satellite males do not become territorial when implanted with testosterone (David Lank, personal communication). Instead, satellite males accelerate and intensify their satellite behaviour. Consequently, testosterone appears to directly turn on genetically encoded information in the brain, which results in the display of distinct male-typical behaviours in a matter of days. Exactly how testosterone can activate two different behavioural repertoires in adulthood remains unknown, but could involve many different mechanisms, including polymorphism in the androgen receptor or genes regulated by the androgen receptor. Whatever the mechanism, the fact that females can exhibit the same behaviours as males suggests that there is not an organizational influence of steroids on the brain during development. In other words, female ruffs are not 'demasculinized' in the same way as female Japanese quail.

Males display significant behavioural variation in at least two other bird species. Buff-breasted sandpipers (*Tryngites subruficollis*), which are related to ruffs, have males with alternative reproductive tactics (85). Lazuli buntings (*Passerina amoena*) have males that exhibit intrasexual variation in reproductive traits similar to *Anolis* lizards and sea gulls, species in which young sexually mature males display female colouration. Yearling males range from a dull brown, female-like plumage to a bright blue, reddish and white plumage (86).

Coloration changes with age so that males aged 2 years or older have bright colouration. These fully mature males settle in prime nesting habitat that attracts females. Mature males are extremely aggressive toward other bright males, including yearlings. As a consequence of this directed aggression, dull yearling males are able to settle in good nesting habitat next to bright adult males and obtain mates, acting like satellite or sneaker males. Nothing is known about the mechanisms underlying variation in male behaviour or morphology in buff-breasted sandpipers or lazuli buntings.

In summary, maternal steroids deposited in the egg yolk mediate the effect of egg laying order on offspring growth, morphology and behaviour in canaries and red-winged black birds. Laying order also has dramatic but different effects on male and female phenotype and survival in house finches. Future studies should determine whether maternal steroids also mediate the effects of egg-laying order in house finches. Another area open for study in these systems is whether the maternal effects on growth, morphology and behaviour of hatchling birds persist and influence reproductive behaviour in adulthood. By contrast to the phenotypic plasticity observed for maternal effects in some species, discrete male phenotypes in the ruff result from hormonal activation of alternative alleles at a single autosomal locus. As we suggested for swordtail fish, a promising area for future work includes cloning and characterizing this polymorphic gene. Investigation of differences in the neurobiology of independent and satellite ruffs, as well as individuals from different positions in the laying order of canaries, blackbirds and house finches, should reveal some fascinating neuroendocrine mechanisms. AVT is a candidate neuropeptide for future study because it modulates aggressive and courtship behaviours in other birds (87, 88).

Mammals

As described briefly in the introduction, there is a surge in testosterone levels in male, but not female, mammals during early development. This endocrine signal has well characterized consequences for sexual differentiation in a number of species (89–91). Interestingly, this endocrine signal also influences neural and behavioural differentiation in adjacent fetuses of both sexes by diffusing through the amniotic fluid. In this section, we review how an individual's intrauterine position, relative to same or opposite sex siblings, influences its reproductive behaviour. Such effects represent an important form of phenotypic plasticity during embryonic development in rodents and possibly humans. We also discuss a mammal that displays plasticity in reproductive behaviour that is due to social interactions in adulthood. In particular, the naked mole rat illustrates how dominance–subordinance relationships can have a dramatic effect on reproductive behaviour.

In mice (*Mus musculus*), male and female fetuses located between two male siblings (2M males and females) are exposed to higher levels of androgens but lower levels of oestrogens than are fetuses located between two female siblings (2F males and females) (92, 93). In accordance with these differences in exposure to exogenous hormones, mice that were located between two males or two females during embryonic development display significant differences in sexual and agonistic behaviour as adults. For example, 2M males are less sexually active and consistently more aggressive than 2F males (Fig. 6). Similarly, 2M females are more aggressive, less attractive to males, mark their cages with urine more frequently, and have longer and more irregular estrous cycles than 2F females (94). Differences in female attractivity might be related to differences in the physiology of preputial glands that produce pheromones (95). Fetuses flanked by a male and a female sibling *in utero* are exposed to intermediate levels of androgens and oestrogens and display patterns of behaviour in adulthood that are intermediate to 2M and 2F individuals of the same sex. Although the intrauterine position phenomenon is observed in a number of litter bearing species such as mice, Mongolian gerbils (*Meriones unguiculatus*) and rats (*Ratus norvegicus*), the exact pattern of intrauterine position effects on behaviour can vary among species (94, 96).

Despite the well-known effects of intrauterine position on reproductive behaviour in rodents, studies of neuroendocrine differences between males (or females) from different intrauterine positions are lacking. However, with the large amount of information on mechanisms underlying sex differences in behaviour in rodents, rapid progress could be made toward understanding the neural basis of continuous variation in reproductive behaviour that occurs with minor variation in exposure to sex steroids within each sex. For example, in the Mongolian gerbil, metabolic capacity was higher in 2M females than in 2F females within regions of the brain that regulate sex behaviour (i.e. the medial part of the anterior hypothalamus) and gonadotropin secretion (i.e. the posterior part of the anterior hypothalamus) (97).

There is also fascinating evidence from studies of twins that the hormonal environment *in utero* may influence neural development in humans (98). Spontaneous otoacoustic emissions (SOAEs) are tonal sounds endogenously produced by the human cochlea. Females, on average, have more SOAEs than males. This sex difference in SOAEs is evident from birth. However, females that have a male twin exhibit half the number of SOAEs observed in females that have a female twin or in females from single births. The number of SOAEs in females with a male twin is comparable to the number of SOAEs detected in males. It was therefore hypothesized that androgens produced by the male twin diffused through the uterus and masculinized the SOAEs of the female twin, similar to the intrauterine position effect seen in rodents.

Discrete variation in reproductive tactics also occurs in mammals. An amazing example of convergent evolution has occurred in naked mole rats (*Heterocephalus glaber*), which display a social structure similar to social ants, bees and termites (99). A single dominant female or 'queen' is the only female that is reproductively active and breeds in a colony of naked mole rats. Furthermore, the queen suppresses reproduction in subordinate females, presumably by aggressive interactions (i.e. shoving) and/or pheromones (100). Removal or death of the queen results in fatal aggression among nonreproductive females that begin ovarian cycles and a struggle to replace the queen (101, 102). Females that are next highest in the dominance hierarchy of the colony vie for the queen's position. Various studies indicate that differences in

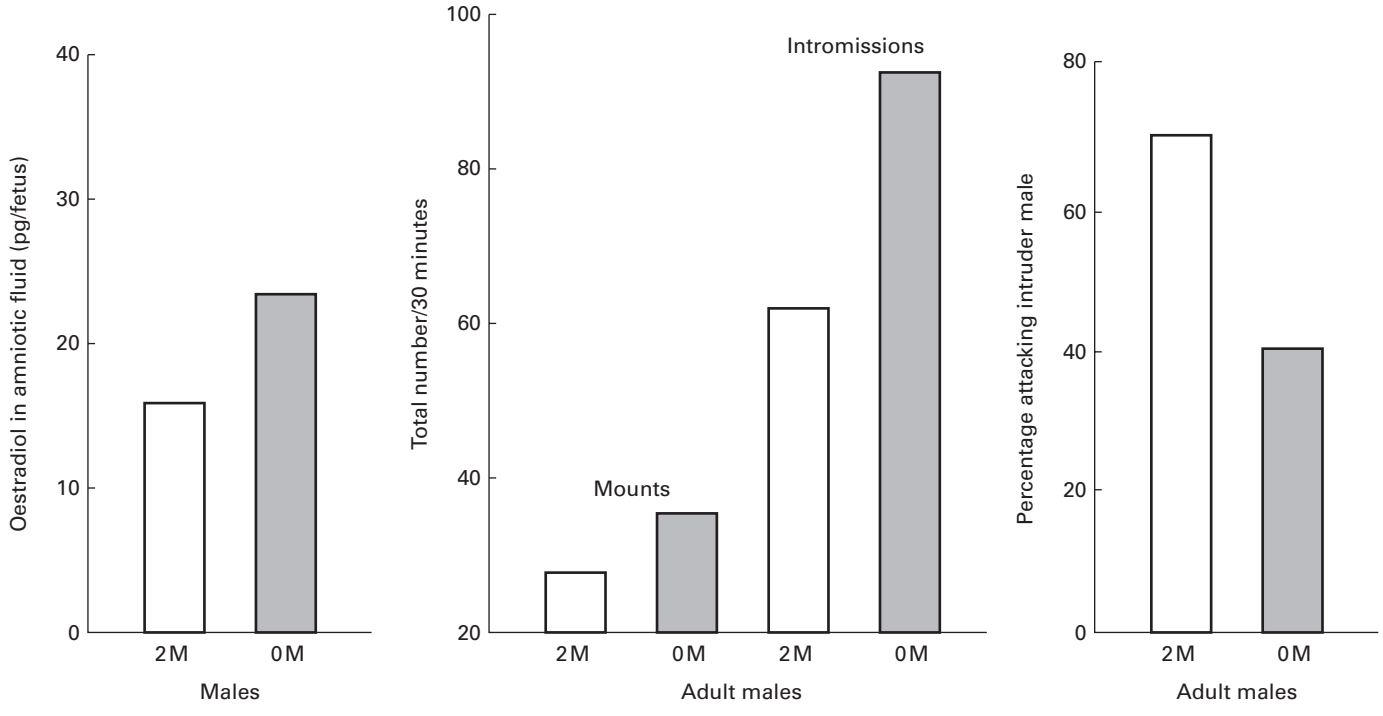

FIG. 6. Effect of intrauterine position on fetal 17β-oestradiol levels (panel on left) in males: 2M indicates males that were located between two males *in utero*, 2F indicates males that were located between two females *in utero*. Effect of intrauterine position on sexual behaviour (i.e. mounts and intromissions in middle panel) and aggressive behaviour (panel on right) in adult male mice are shown. After (93).

the activity of the hypothalamic-pituitary-gonadal axis underly these alternative reproductive strategies.

Queens, for example, are more sensitive to exogenous GnRH than are nonreproductive females. Injection of low doses of GnRH stimulate a large increase in plasma luteinizing hormone (LH) levels in queens but produce a much smaller effect in nonreproductive females (103). In agreement with these results, nonreproductive females normally have low LH and progesterone levels compared to queens. This study also showed that repeated injections of the lowest dose of GnRH in nonreproductive females raise plasma levels of LH to those found in queens injected just once with the same low dose. Suppression of reproductive cycles and ovulation in nonbreeding females may be due to social inhibition of hypothalamic GnRH secretion. In agreement with this hypothesis, nonreproductive females begin cycling when removed from their colony and the suppressive influence of their queen (103). Reproductive suppression may be mediated by pheromones produced by the queen and/or overt physical aggression (i.e. shoving) directed at nonreproductive females.

In any case, morphological differences between queens and nonreproductive females in the naked mole rat are analogous to the queen–worker size dichotomy observed in social insects (104). In particular, naked mole rat queens have significantly longer lumbar vertebrae and torsos than do nonreproductive females. Interestingly, litter size increases from an average of seven pups in a queen's first litter to an average of 12–13 pups in her fourth litter. Moreover, established queens can produce litters containing up to 28 pups. This dramatic increase in fecundity in female naked mole rats is associated with an elongation of the torso upon attainment of breeding status. Gastrointestinal hypertrophy also occurs in queens and may be an adaptation to support larger litter sizes. The mechanisms responsible for these changes in morphology are currently unknown but most likely involve a suite of endocrine and neuroendocrine changes, including the aforementioned changes in the hypothalamic-pituitary-gonadal axis.

Overall, mammals appear to be quite sensitive to environmental perturbations that influence intrasexual variation in behaviour. This phenotypic plasticity is evident in rodent embryos that are susceptible to small variations in hormone levels from exogenous sources and in adult naked mole rats that are dramatically influenced by social interactions. A productive area for future work will be the neural basis of intrauterine position effects in rodents (and humans). The advent of cDNA microarrays will be useful for the identification of genes that are differentially regulated by environmental factors. Although we did not discuss them, studies using cDNA microarrays will also be a fruitful area for identifying genetic polymorphisms in reproductive behaviour (105). The pace of such studies could be very rapid, considering that the sequencing of the mouse genome is nearing completion and that many inbred strains of mice are commercially available.

Summary and conclusions

In this review, we have illustrated a few of the genetic, cellular, hormonal, and/or neural mechanisms underlying intrasexual variation in behaviour (Table 1). Such behavioural variation ranges from the discrete alternative phenotypes observed in plainfin midshipman, side-blotched lizards and ruffs to the continuous variation observed with incubation temperature effects in leopard geckos and intrauterine position effects in rodents. A general dichotomy of mechanism may underlie these extremes. For example, it is interesting to hypothesize that a single major genetic factor with alternative alleles regulates a whole suite of traits in most species with discrete alternative phenotypes. Molecular cloning and characterization of such genes may be feasible in species such as the swordtail and the ruff that already have a defined genetic polymorphism. In contrast, it appears that many factors may produce subtle variation in the levels of a major regulatory factor (i.e. sex steroid hormones) in species with continuous variation in behaviour.

We have also shown that alternative reproductive strategies are taxonomically widespread in vertebrates (Table 1). These alternative reproductive strategies may be fixed (i.e. genetically based) as in swordtails and ruffs or developmentally plastic as in leopard geckos, rodents and frogs. By plastic, we mean that each individual has the potential to develop or display more than one behavioural phenotype. Within this category are further subdivisions. Some behavioural phenotypes are established by environmental factors during early ontogeny, whereas others are the result of developmental transitions from one strategy early in life to another later in life. Still other strategies are truly facultative with individuals displaying different behaviours in different social contexts.

An important caveat concerning our review of the literature is that current examples of alternative reproductive tactics are biased toward males. This bias may reflect the fact that most studies of intrasexual variation in behaviour have focused on males. It is possible, however, that this male bias may reflect a real difference in the frequency of alternative reproductive strategies between the sexes. This is potentially a viable explanation because sexual selection often acts more strongly on males than on females. An analysis of the Bateman gradient indicates that a male's reproductive success generally increases with the number of females that he fertilizes. In

Table 1. Summary of Species that Display Intrasexual Variation in Reproductive Behaviour. Species are categorized according to their taxonomic group.

			Regulatory factors		
Group	Animal	Behaviour	Genetic polymorphism/ Phenotypic plasticity	Hormonal factors	Cellular/neural factors
Fish	Plainfin midshipman	Parental/ vocal	?	Androgens	GnRH neurones, AVT, isotocin, vocal circuits, sonic muscles
	Swordtail	Courtship	Y-linked polymorphism	Androgens	LHRH neurones
Amphibians	Strawberry poison dart frog	Parental	?	?	?
	Bull frog	Vocal	Phenotypic plasticity	Androgens/oestrogens	AVT, AVT receptor
	Cricket frog	Vocal	Phenotypic plasticity	Androgens/glucocorticoids	AVT in nucleus accumbens
	Rough-skinned newt	Mating	Phenotypic plasticity	Glucocorticoids	GABAergic system
Reptiles	Side-blotched lizard	Territorial/ mate guarding	Polymorphism and phenotypic plasticity	Androgens	?
	Tree lizard	Territorial	?	Androgens/progestins/ glucocorticoids	?
	Leopard gecko	Territorial/mating	Phenotypic plasticity	Androgens/oestrogens	Metabolic capacity and volume of various limbic nuclei
Birds	Canaries and blackbirds	Begging and aggression by hatchlings	Phenotypic plasticity	Androgens	?
	Ruffs	Territorial/mating	Autosomal polymorphism	Androgens	?
	Buff-breasted sandpipers	Territorial/mating	?	?	?
Mammals	Mice	Mating/aggression	Phenotypic plasticity	Androgens/oestrogens	?
	Naked mole rats	Mating/aggression	Phenotypic plasticity	Oestrogens/progestins/ glucocorticoids	GnRH, LH
	Humans	Hearing	Phenotypic plasticity	Androgens?/oestrogens?	Cochlea

For each species, reproductive behaviours that vary and the regulatory factors that alter those behaviours or that differ between individuals that differ in behaviour are listed. Regulatory factors indicate (i) whether this behavioural variation is due to genetic polymorphism or phenotypic plasticity; (ii) hormonal factors that alter behaviour or that differ between individuals; and (iii) the cellular/neural factors that alter behaviour or that differ between individuals. GnRH, gonadotropin releasing hormone; AVT, arginine vasotocin; LHRH, luteinizing hormone-releasing hormone.

contrast, a female's fecundity usually does not increase with the number of mates she obtains, but is often limited by the number of eggs she produces (106, 107). However, this is not always the case, as sexual selection may be stronger on females in species with sex-role reversal (108). Studies of intrasexual variation in female behaviour and its underlying mechanisms in such species are an exciting area for future research.

In summary, intrasexual variation in behaviour adds another level of complexity to studies of brain organization and function. Such information is essential for a clear picture of the unique and conserved mechanisms underlying sex and individual differences in behaviour in vertebrates as a whole. For example, common mechanisms underlying intrasexual variation include variation in sex steroid hormone levels and AVT neurophysiology. Furthermore, although there may be conservation of an underlying hormonal mechanism such as sex steroids in all vertebrates, completely different factors may influence levels of sex steroids (i.e. incubation temperature in leopard geckos and intrauterine position in rodents). Ultimately, we envision that neurobehavioural models of this sort will help us better understand the tremendous diversity observed in human reproductive and agonistic behaviour.

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