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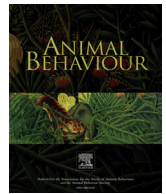
- Chemical profiles differ substantially between species across strepsirrhines.
- Urine markers express more urinary compounds than do nonurine markers.
- Signal richness is linked to various aspects of the focal species' socioecology.
- Chemical signals evolve gradually and at fast rates in strepsirrhines.

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Socioecological and phylogenetic patterns in the chemical signals of strepsirrhine primates

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Our understanding of chemical signals in mammals derives principally from studies in which researchers examine signal structure or function within a single species. Despite the unique information to be gained from applying comparable methods across multiple species, comparative studies of chemical signals are extremely limited. Here, we review the available literature on the evolution of chemosignals in male and female strepsirrhine primates (galagos, lorises and lemurs), all of which rely heavily on chemical communication. We draw from a few case studies, but focus our review on two comparative studies. In one, researchers examined the volatile chemical composition of urinary signals across 12 species representing most families within Strepsirrhini, including six 'urine-marking' species and six glandular or 'nonurine-marking' species. In the other, researchers examined the volatile chemical composition of glandular signals in eight *Eulemur* species differing in social or dominance structure. We highlight five findings. (1) Regardless of the scent source, chemical profiles differ substantially between species, providing reliable species 'scent signatures'. None the less, (2) urine markers express more compounds and have more distinguishable species scent signatures in their urine than do nonurine markers, suggesting specialization of function. Within *Eulemur* (3) chemical richness is greater in multimale–multifemale species than in pair-bonded species. Moreover, (4) whereas chemical richness of male signals is greater in sexually codominant species, chemical richness of female signals is greater in female-dominant species. Together, the findings from both comparative studies, coupled with case studies, suggest that signal richness is linked to some aspect of the focal species' socioecology. Lastly, (5) regardless of the scent source, strepsirrhine chemosignals evolve gradually over time, but at fast rates and homogeneously within different lineages. Comparative studies reveal patterns that cannot be detected from the single-species approach and are therefore critical for providing new insight into the function and evolution of olfactory signals.

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Chemical signals convey information about individuals and their physiological states (Wyatt, 2014). As in other mammals, intraspecific studies on the composition of primate chemical signals (reviewed in e.g. Drea, 2014; Epple, 1986; Michael, Bonsall, & Zumpe, 1976) have shown that these chemical signals can contain information about the signaller's sex (Belcher, Smith, Jurs, Lavine, & Epple, 1986; Crewe, Burger, Roux, & Katsir, 1979; Greene & Drea, 2014; Hayes, Morelli, & Wright, 2004; Penn et al., 2007; Scordato, Dubay, & Drea, 2007; Setchell et al., 2010), reproductive state

(Crawford, Boulet, & Drea, 2011; Greene & Drea, 2014; Hayes, Morelli, & Wright, 2006; Scordato et al., 2007), identity (Palagi & Dapporto, 2006; Penn et al., 2007; Scordato et al., 2007; Smith, Tomlinson, Mlotkiewicz, & Abbott, 2001) and 'quality' (as estimated by genetic diversity: Boulet, Crawford, Charpentier, & Drea, 2010; Charpentier, Boulet, & Drea, 2008; as estimated by major histocompatibility complex genotype: Setchell et al., 2011), as well as the genetic relatedness between individuals (Boulet, Charpentier, & Drea, 2009; Charpentier et al., 2008; Morelli et al., 2013).

In contrast to the emphasis placed on intraspecific studies, there have been exceptionally few mammalian studies in which researchers used a comparative approach to analyse chemical data (Belcher et al., 1986; Decker, Ringelberg, & White, 1992; Zabar, Richardson, & Wyllie, 2005). Comparative studies can

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be methodologically challenging (delBarco-Trillo, Burkert, Goodwin, & Drea, 2011; Drea et al., 2013), but can provide a wealth of information about species differences relevant to understanding broader socioecological patterns, as well as unique insights into the evolution of chemical signals across different phylogenetic scales (Symonds & Elgar, 2008). Here, we review recent comparative studies on the volatile composition of chemical signals in strepsirrhine primates to elucidate whether socioecological factors correlate with the composition of chemical signals and to uncover the mode and speed of chemical signal evolution.

CHEMICAL SIGNALS IN STREPSIRRHINE PRIMATES

The Strepsirrhini clade is a diverse suborder of primates that comprises members of Lorissidae, Galagidae, Cheirogaleidae, Daubentonidae, Lemuridae, Lepilemuridae and Indriidae. Defined by their wet nose or rhinarium, strepsirrhines are a macrosomatic group in which all species have highly developed chemoreceptive organs (Epple, 1986; Meisami & Bhatnagar, 1998; Schilling, 1979, 1980; Stephan, Frahm, & Baron, 1981). Most strepsirrhine species use more than one type of chemical signal for communication purposes, including saliva, urine, faeces and secretions expressed in various body areas (head, neck, chest, forelimb and anogenital area; Schilling, 1979). This rich array of scent signals is accompanied by various, sometimes visually conspicuous, modes of deposition or scent dispersal, such as the ritualized 'stink fights' of male ring-tailed lemurs, *Lemur catta* (Jolly, 1966).

Urine marking, one of the most cryptic means of scent deposition, serves as the main type of chemical communication in many strepsirrhines, particularly in nocturnal species (Schilling, 1979). By contrast, it does not seem to have a significant semiochemical function in other species, such as most lemurs (e.g. *Phaner* spp. and *Eulemur* spp.) and the indri, *Indri indri* (Schilling, 1979). The chemical composition of urine can be very complex. In several mammalian species (Burger, 2005; Jemiolo, Xie, & Novotny, 1991), including the aye-aye, *Daubentonia madagascariensis* (delBarco-Trillo, Harelimana, Goodwin, & Drea, 2013), compounds can be added to urine from secretory structures along the urogenital tract. The addition of compounds suggests that the chemical composition of urine is not completely tied to the physiological process of excretion, and that the chemical profiles of different species can thus evolve in response to the communication requirements in each species (delBarco-Trillo et al., 2013; Burger, 2005; Jemiolo et al., 1991; Weinhold & Ingersoll, 1988).

As in many other mammals, the glandular structures of strepsirrhine primates are varied and can be sexually differentiated, with males possessing scent organs that are either absent in females or better developed than those of females (e.g. Montagna & Yun, 1962). In some cases, however, this typical pattern of sexual differentiation is reversed between the sexes. For instance, the genital and perianal glands in *Eulemur* spp., located in folds around the genital and the anal regions (Hill, 1953; Montagna & Yun, 1962), are morphologically more complex in females than in males (delBarco-Trillo, Sacha, Dubai, & Drea, 2012). Glandular morphology can thus be consistent with other features of sexual reversal that exist within this clade (Drea, 2007; Drea & Weil, 2008).

The diversity evidenced in strepsirrhine chemical communication is complemented by great diversity in strepsirrhine socioecology, even between closely related species (Colquhoun, 2011; Schilling, 1979). Strepsirrhines are thus an interesting group in which to address comparative questions, as both the animals' reliance on chemical signals and the features of their social and physical environment have the potential to affect the evolution of chemical signals.

COMPARATIVE STUDIES REVEAL 'SPECIES SCENT SIGNATURES'

In the first study to examine how the composition of chemical signals might differ between strepsirrhine species, Hayes et al. (2004) compared the volatile composition of secretions deriving from the anogenital area in two phylogenetically distant species (*L. catta* and the Coquerel's sifaka, *Propithecus coquereli*). As anticipated, the authors found that the chemical profiles of these two species' secretions were chemically distinct. Given that these species differ in their glandular structures (notably, the scrotal gland of male *L. catta* is species specific; Montagna & Yun, 1962) and that different glandular secretions are chemically distinct even within a species (Scordato et al., 2007), it is difficult to interpret the nature of these chemical differences. Comparable morphological derivation constitutes only one of the multiple challenges facing broadly comparative studies.

Since then, only two studies have used a comparative approach to address the evolution of chemical signals across the Strepsirrhini. In the first of these studies, the authors (delBarco-Trillo et al., 2011) handled the issue of morphological differences across species by comparing the volatile compounds expressed in urine. They addressed differences between 12 species by comparing the volatile composition of urine in six species that rely primarily on urine for chemical communication ('urine markers') with that of six species that do not seem to rely on urine, but instead rely on glandular secretions for communication ('nonurine markers'). In the second of these studies, the authors (delBarco-Trillo et al., 2012) focused on glandular secretions within the same genus, *Eulemur*, such that all eight species examined shared similar genital and perianal glandular morphologies, but differed in important aspects of their social and dominance structures. As we shall see, even when examining the same class of odorants (i.e. those derived from the same source), both of these studies revealed profound species differences.

In the 'urinary signal' study (delBarco-Trillo et al., 2011), the 12 species were selected to represent most of the families in the strepsirrhine phylogeny. Species differences in their urinary chemical profiles were remarkable in that none of the total of 74 volatile compounds detected were shared by all species and 70% of the compounds detected were expressed in only one species.

When comparing the subset of 'urine markers' against the subset of 'nonurine markers,' the number of volatile compounds was found to be greater in the former than in the latter (delBarco-Trillo et al., 2011). This finding held true whether considering all compounds detected in the species under study or only those compounds that have been reported elsewhere (i.e. in any mammalian species) as having a semiochemical function (delBarco-Trillo et al., 2011). In addition to having the most complex urinary chemical profiles, urine-marking species had 'scent signatures' that were the most dissimilar from one another; nonurine markers shared more similar chemical profiles. Together, these findings show that reliance on a chemical signal for social communication can lead to an increase in its chemical richness and greater diversification from other species.

In the study involving the eight species of *Eulemur* (delBarco-Trillo et al., 2012), the composition of volatile compounds in glandular signals also differed by species. At the individual level, the numbers of compounds expressed in genital and perianal secretions were similar and positively correlated, such that as the number of compounds in the genital secretion of one animal increased, so too did the number of compounds in that animal's perianal secretion. Despite expressing similar numbers of compounds and despite close physical proximity, the perianal and genital glandular fields produce unique chemical profiles. Species

'scent signatures' were found, independently, in both types of secretions.

Although no sex differences were detected in urinary signals (delBarco-Trillo et al., 2011), the glandular chemical profiles were significantly different between male and female *Eulemur*, and also between the breeding and the nonbreeding seasons (delBarco-Trillo et al., 2012). Thus, there can still be shared chemical features that code for sex and reproductive state across species, even though the chemical profiles of species are distinctly different from each other. Lastly, from earlier discrimination studies conducted by Harrington (1979), it is clear that at least some strepsirrhines are capable of distinguishing between their own species' scent and that of other sympatric species. Such behavioural studies suggest that the chemical differences described above as 'species scent signatures' are salient to the animals and, hence, functional.

SOCIOECOLOGICAL PATTERNS IN CHEMICAL SIGNALS

One potential interpretation for the presence of more distinctive urinary signatures among urine markers than among nonurine markers relates to the socioecological differences that exist between these two groups (delBarco-Trillo et al., 2011; Schilling, 1980). Urine markers are, in most cases, nocturnal and relatively solitary, particularly when foraging, whereas nonurine markers have either diurnal or cathemeral activity patterns and live in socially integrated groups of varying size (Schilling, 1979, 1980). Urine marking may sufficiently meet the communication requirements of a low-visibility environment in which animals interact infrequently. By contrast, scent marking in diurnal and social species is often performed in the immediate presence of conspecifics. Increased demand for more conspicuous or even multimodal signalling could have selected for a shift towards the use and elaboration of glandular signals in diurnal and social species and may have eventually led to a reduction in the use and complexity of urine in such species (delBarco-Trillo et al., 2011).

A relevant test case in this regard is presented by the sifakas (*Propithecus* spp.). Sifakas exhibit an unusual socioecology for their phylogenetic placement, as they are diurnal and social, but evolved in a clade comprising nocturnal and primarily solitary species. The olfactory repertoire of the sifakas reflects components of both taxonomic groups. Like their close relatives, sifakas maintain olfactory reliance on urine, but they produce comparatively richer urinary signals (delBarco-Trillo et al., 2011; Greene & Drea, 2014). Like other diurnal and social strepsirrhines, however, sifakas also rely on various, specialized glandular secretions in intraspecific communication. They deposit secretions from multiple glands together, using a suite of conspicuous behavioural postures, and these secretions are associated with permanent, visible signs, thereby producing composite, multimodal signals (Lewis, 2006; Patel, 2009). Chemical analyses of the genital secretions alone reveal that sifakas express hundreds of chemical compounds that encode a rich array of information about the signaller (Greene & Drea, 2014; Hayes et al., 2006; Morelli et al., 2013). Thus, evolutionary pressures within a diurnal and more socially complex lifestyle may have selected for an increase in olfactory complexity in both urinary and glandular modalities.

Given that the complexity of vocal signals has been linked to social complexity in various species, including primates (Freeberg, Dunbar, & Ord, 2012), one could posit that the complexity of chemical signals might also relate to social complexity in those species that rely heavily on olfactory communication. This prediction, however, has not received much experimental attention. An additional focus of the 'glandular signal' study in *Eulemur*, therefore, was to examine how socioecological differences between

species might correlate with the composition of their chemical signals (delBarco-Trillo et al., 2012).

Eulemur species are socioecologically diverse. Those selected for study differ in terms of both their social complexity (pair-bonded versus multimale–multifemale groups) and their dominance structure (female-dominant species versus sexually egalitarian or codominant species). The complexity of perianal secretions was found to be significantly greater in species that form multimale–multifemale groups than in those that live in pairs. Comparable to the evolutionary patterns observed in vocal signals, the increased social interactions in multimale–multifemale groups may have selected for increased chemical signal complexity to accommodate increased intragroup communication.

Regarding the relationship between chemical complexity and dominance structure in *Eulemur*, the number of chemical compounds in both genital and perianal secretions was found to be greater in sexually codominant species than in female-dominant species (delBarco-Trillo et al., 2012). This chemical difference between female-dominant and codominant species is due mostly to the greater number of compounds found in male secretions among sexually codominant species. Moreover, a sexual reversal in signal complexity exists depending on dominance structure. Males have richer chemical secretions in sexually codominant species, whereas females express more chemically complex secretions than males in female-dominant species.

The general relationship between social complexity and chemical complexity also becomes apparent when one considers the olfactory communication repertoire of *L. catta*. *Lemur catta* is diurnal, spends a significant portion of its time in visually open, terrestrial habitats, and is the most socially complex of the strepsirrhine primates, living in relatively large multimale–multifemale groups (Sauther, Sussman, & Gould, 1999) that exceed the size of *Eulemur* groups (Curtis & Zaramody, 1999). *Lemur catta* arguably possesses one of the most complex olfactory repertoires of any of the strepsirrhines (Schilling, 1974), which, like that of sifakas (Lewis, 2006), includes the use of composite, multimodal signals (Drea & Scordato, 2008). The chemistry of their volatile urinary (delBarco-Trillo et al., 2011) and glandular signals (Boulet et al., 2009, 2010; Charpentier et al., 2008; Crawford et al., 2011; Hayes et al., 2004; Palagi & Dapporto, 2006; Scordato et al., 2007) has been well characterized. Notably, whereas the genital secretions of males and females in any species of *Eulemur* examined to date contain fewer than 30 compounds (delBarco-Trillo et al., 2012), hundreds of compounds have been detected in the genital secretions of male and female *L. catta* (Boulet et al., 2009; Scordato et al., 2007). These comparisons suggest a relationship between chemical complexity and social complexity; however, as noted above, this comparison is complicated by the different glandular morphologies. Unfortunately, there are no other extant members of *Lemur* to allow a formal comparative test. In this regard, chemical studies of *Hapalemur*, in which animals live in smaller social groups (Tan, 1999), but share similar glandular morphologies with *Lemur* (Simons & Rumpler, 1988), would be enlightening.

Although group size can be an informative metric of sociality in species characterized by large social systems, for species living in small social groups, the quality of relationships may be a more valuable proxy for estimating complexity (Dunbar & Shultz, 2007). Sifakas again provide an interesting test, in this case for understanding the links between social and olfactory signal complexity. Sifakas reside in small, stable family groups, comprising a dominant breeding pair and associated family members (Patel, 2009). Breeding pairs can have a relatively long tenure, often living and reproducing together for years. Recently, researchers have shown that genital signalling in sifakas reflects the social bond that exists within breeding pairs (Greene & Drea, 2014). Moreover, the

strength of the social bond between members predicted patterns in scent deposition and modestly predicted patterns in odorant chemistry. Notably, strongly bonded pairs, as evidenced by past reproductive success, scent-marked less often, but produced more similar chemical profiles than weakly bonded or reproductively unsuccessful pairs. That the strength of social bonds was reflected in chemical complexity suggests another means by which socioecology may relate to the evolution of olfactory signals.

EVOLUTION OF CHEMICAL SIGNALS IN STREPSIRRHINES

Beyond identifying the socioecological factors that might shape chemical signals, an additional objective for both the urinary signal and glandular signal studies was to determine the manner and rate of chemical signal evolution at different phylogenetic scales. Notably, differences in signal complexity between urine markers and nonurine markers could be the result of different phylogenetic histories in these two groups (delBarco-Trillo et al., 2011). Likewise, the study of glandular signals within the genus *Eulemur* is relevant for determining whether some of the phylogenetic patterns observed across strepsirrhines are also apparent at a more restricted phylogenetic scale.

Given that nonurine markers form a relatively recent subclade within Strepsirrhini (Horvath et al., 2008), the phylogenetic distances between nonurine markers are often smaller than those between urine markers (delBarco-Trillo et al., 2011). Indeed, there is a positive correlation between chemical distances and phylogenetic distances between strepsirrhine species, indicating that, with sufficient genetic distance, any two species will differ in their chemical profiles, no matter how much they rely on urine for chemical communication.

More importantly, the significant and positive association between urinary chemical distances and phylogenetic distances across strepsirrhine species supports a gradual mode of evolution. As has been described for species evolution, two different modes of evolution, i.e. gradual and saltational, have been proposed for the evolution of chemical signals (Symonds & Elgar, 2008). Theoretical and empirical support, derived from studies of different insect clades, exists for both gradual (Symonds & Wertheim, 2005) and saltational (Symonds & Elgar, 2004) modes of chemical signal evolution. A saltational mode of evolution is expected when small changes in the chemical profile of a species can decrease the functionality of that chemical signal (e.g. a pheromone involved in sexual attraction). Significant changes to the chemical profile may thus occur during the first stages of speciation to favour assortative mating, but not during later stages (Symonds & Elgar, 2004, 2008), creating a pattern in which chemical distances are not correlated with phylogenetic distances. In contrast, we expect a gradual mode of chemical signal evolution when gradual changes can accumulate in a chemical signal over time without decreasing its signalling function (Symonds & Elgar, 2008; Symonds & Wertheim, 2005).

In accordance with the gradual mode of evolution detected in the urinary profiles across strepsirrhines (delBarco-Trillo et al., 2011), a gradual mode of chemical signal evolution is also evident within the genus *Eulemur*, in analyses of the chemical composition of both genital and perianal secretions (delBarco-Trillo et al., 2012). The two observations that a gradual mode of evolution is apparent (1) at both large and small phylogenetic scales and (2) for both urine and glandular secretions would seem to indicate that a gradual mode of evolution may be the norm in the evolution of chemical signals in strepsirrhines, and possibly in other mammalian groups. It must be noted, however, that these comparative analyses on whole chemical profiles cannot be extrapolated to understand the evolution of particular compounds.

The gradual evolution and significant species differences observed in *Eulemur* (i.e. at a small phylogenetic scale) suggest that chemical signals in strepsirrhines evolve at fast rates. To determine the relative speed at which chemical profiles evolve in strepsirrhines, one can estimate the probability that compounds detected in extant strepsirrhine species would also have been present in ancestral species (delBarco-Trillo et al., 2011). One approach to estimate the presence of compounds in ancestral states is the implementation of a stochastic mutational mapping analysis, a probabilistic approach that uses the information about presence and abundance of compounds in extant species to determine the probability of each of these compounds being found in each node in the phylogenetic tree (Bollback, 2006). This approach, which had previously been used to study the evolution of sex pheromones in *Bactrocera* spp. of flies (Symonds, Moussalli, & Elgar, 2009), was also applied to the urinary chemical profiles in strepsirrhines (delBarco-Trillo et al., 2011). If a compound was considered likely to be found in an ancestral state if the calculated probability were 0.5 or higher, only 18% of volatile compounds met this criterion (delBarco-Trillo et al., 2011). Of course, choosing a more conservative approach that considered probabilities greater than 0.5 would have led to the percentage of volatile compounds likely to be found in ancestral states being even lower than 18%. Regardless, the large number of estimated changes between the chemical profiles of ancestral and extant species indicates that there is a high turnover of volatile compounds in the urine of strepsirrhines. In addition, the speed at which chemical profiles evolve does not seem to differ between the phylogenetic clade containing urine markers and that containing nonurine markers (delBarco-Trillo et al., 2011). We can thus conclude that chemical signals in strepsirrhines evolve gradually, at fast rates, and homogeneously across different lineages.

CONCLUDING REMARKS

For decades, the comparative approach has been an essential tool for examining broad evolutionary patterns. In the field of animal communication, comparative studies have been particularly successful in furthering our understanding of the structure, complexity and functionality of vocal signals. In contrast, beyond consistent documentation of species differences in olfactory profiles, across widely divergent taxonomic groups, we have a limited understanding of the socioecological and phylogenetic forces that shape the evolution of chemical signals within any taxon. Available data in strepsirrhine primates hints at a connection between chemosignal complexity and social complexity, but more research is needed. The comparative approach, applied to the chemical analysis of animal scents, will illuminate the functionality and evolution of chemical signals in a manner unavailable to the single-species approach. With additional technological advances in analytical chemistry, to allow integrated examination across a broader sweep of chemosignals, coupled with software development, particularly in automation procedures and pattern recognition programs, we anticipate that evolutionary biologists will increasingly delve into addressing these challenging questions.

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