

INVITED REVIEW

Advances in our understanding of mammalian sex-biased dispersal

L. J. LAWSON HANDLEY*† and N. PERRIN†

*Theoretical and Molecular Population Genetics Group, Department of Genetics, University of Cambridge, Downing Street, Cambridge, CB2 3EH, UK, †Department of Ecology and Evolution, University of Lausanne, CH-1015 Lausanne, Switzerland

Abstract

Sex-biased dispersal is an almost ubiquitous feature of mammalian life history, but the evolutionary causes behind these patterns still require much clarification. A quarter of a century since the publication of seminal papers describing general patterns of sex-biased dispersal in both mammals and birds, we review the advances in our theoretical understanding of the evolutionary causes of sex-biased dispersal, and those in statistical genetics that enable us to test hypotheses and measure dispersal in natural populations. We use mammalian examples to illustrate patterns and proximate causes of sex-biased dispersal, because by far the most data are available and because they exhibit an enormous diversity in terms of dispersal strategy, mating and social systems. Recent studies using molecular markers have helped to confirm that sex-biased dispersal is widespread among mammals and varies widely in direction and intensity, but there is a great need to bridge the gap between genetic information, observational data and theory. A review of mammalian data indicates that the relationship between direction of sex-bias and mating system is not a simple one. The role of social systems emerges as a key factor in determining intensity and direction of dispersal bias, but there is still need for a theoretical framework that can account for the complex interactions between inbreeding avoidance, kin competition and cooperation to explain the impressive diversity of patterns.

Keywords: competition, cooperation, gene flow, inbreeding avoidance, kin selection, mating systems, sex-biased dispersal

Received 20 June 2006; revision accepted 1 September 2006

Introduction

Dispersal of individuals from the natal group in order to breed is one of the most important aspects of an organism's life history. Among animals, there are normally large differences between the sexes in terms of distances travelled during dispersal and/or dispersal rates. Sex-biased dispersal (SBD) therefore has important consequences for the genetic makeup of populations (Clobert *et al.* 2001).

In the early 1980s, analyses of general patterns of sex-biased dispersal in both mammals and birds set the framework for subsequent research on the predictions and theory of SBD (Greenwood 1980; Dobson 1982). Greenwood (1980) reviewed mating systems and dispersal strategies and

found that male-biased dispersal (MBD), and female philopatry were the norm in mammals, whereas birds tended to exhibit female-biased dispersal (FBD) and male philopatry. This observation led Greenwood to hypothesize that direction of dispersal bias was tightly linked to the mating system, with female-defence polygyny, a common breeding system of mammals, leading to male-biased dispersal, and resource-defence monogamy, more typical of birds, favouring dispersal by females. Since then, this important topic has been the focus of extensive theoretical and empirical work, and many papers have attempted to explain the patterns of SBD. The main evolutionary models invoke inbreeding avoidance (Bengtsson 1978; Packer 1979; Dobson 1982; Waser *et al.* 1986; Pusey 1987; Clutton-Brock 1989; Wolff 1994; Perrin & Mazalov 2000), or kin selection arguments including local resource competition (LRC, Greenwood 1980; Clarke 1978), local mate competition (LMC, Hamilton

Correspondence: Lori Lawson Handley, Fax: +44 (0)1223 333992; E-mail: ljl27@cam.ac.uk

1967; Dobson 1982; Moore & Ali 1984), and more recently, cooperative behaviour among kin including local resource enhancement (LRE, e.g. Perrin & Lehmann 2001; Le Galliard *et al.* 2006). Many variations on these models and proximate explanations for SBD have also been invoked, all of which can be quite bewildering to newcomers to the field.

The study of sex-biased dispersal is inherently multidisciplinary, combining complex evolutionary theory with population dynamics modelling and long-term field studies of animal behaviour. More recently, the field has been augmented by advances in molecular genetic techniques that allow investigation of how individual movements are translated into effective dispersal and gene flow. Our aims in this review are to synthesize the major theoretical models that address the evolutionary causes of dispersal for those working in population genetics, to encourage direct testing of evolutionary hypotheses for SBD, and to provide guidelines for measuring sex-biased dispersal using molecular data. We begin with an appraisal of our theoretical understanding of the evolutionary causes of SBD. We then turn to a review of empirical data of SBD in mammals and comment on proximate explanations and modes of SBD. Finally, we discuss recent advances in statistical genetics that allow us to measure both direction and rate of sex-biased dispersal and gene flow.

Evolutionary explanations for sex-biased dispersal: advances in our theoretical understanding

Dispersal strategies can evolve under a large variety of selective pressures, being opposed by some of them, and favoured by others. Selective pressures that *do not* favour dispersal are threefold. First, dispersers may incur significant *mortality costs* when crossing unfavourable habitats to reach suitable patches. In small mammals for example, survival rate can be almost 50% lower for dispersers than for philopatric individuals (Johnson & Gaines 1990). Second, *familiarity with natal area* becomes important when resource acquisition involves complex interactions with the environment. Immigrants reaching a suitable patch are likely to be at a disadvantage when competing with residents for a limiting resource. Third, the benefits of *kin cooperation* may provide further competitive advantages to residents, and thereby promote philopatry. Cooperation should help to acquire or defend mates or resources, but also prevent unrelated competitors joining the group (e.g. Le Galliard *et al.* 2006). This pressure, which is likely to play a role in all social species, might become crucial in societies that use good kin-recognition abilities (as evidenced in several species groups, such as mammals, e.g. house mice, Kareem & Barnard 1986; chimpanzees, Parr & de Waal 1999; birds, Nakagawa & Waas 2004; fish, e.g. migratory charr, Fraser *et al.* 2004) to build cooperative interactions (Perrin & Lehmann 2001; Lehmann & Perrin 2002).

Selective pressures that *do* favour dispersal are also threefold. The first is set by spatio-temporal variability in *resource availability*. Provided resources available in the new patch are not correlated to those in the natal patch (i.e. when autocorrelation is weak), it pays to leave natal patches when resources are locally depleted, or when there is a risk of extinction (Comins *et al.* 1980). Second, by dispersing, individuals avoid *kin competition* for mates (LMC) or resources (LRC), since leaving natal patches frees these resources for relatives (Hamilton & May 1977; Clarke 1978). The third pressure is set by *inbreeding avoidance*. Dispersal lowers the risk of mating with relatives, and hence the cost of inbreeding depression (Cockburn *et al.* 1985; Motro 1991; Gandon 1999; Perrin & Mazalov 1999).

The evolutionary stable patterns of dispersal result from a balance between the above forces. As these forces are often sex-specific, equilibrium values are likely to differ between males and females. Mating systems are thus a priori expected to affect dispersal patterns. Among the forces *opposing* dispersal, familiarity with natal area is crucial for the sex responsible for territory acquisition and defence (Greenwood 1980), namely males in resource-defence systems (many birds and some mammals), but females in female-defence systems (many mammals). In social species, resource acquisition relies on kin cooperation. The building of social bonds among members of one sex is expected to reinforce the pressure against dispersal in this sex, and hence contribute to sex-biased dispersal. Cooperation among related males may help access to territory and mates in resource defence systems (e.g. red grouse, Watson *et al.* 1994). In female-defence systems, cooperation may occur among related females, for example to rear offspring (e.g. lions, Packer & Pusey 1987; Townsend's voles, Lambin 1994; grey mouse lemur, Radespiel *et al.* 2001, 2003) but also among related males, for example to acquire and defend females (e.g. lions, Packer & Pusey 1987). Mating systems also play a role in *favouring* SBD since limiting resources are often sex-specific (Perrin & Mazalov 2000). In female-defence systems for instance, local mate competition in males is likely to exceed local resource competition in females, so that kin competition avoidance is expected to induce male-biased dispersal (Perrin & Mazalov 2000).

Inbreeding avoidance should also contribute to sex-biased dispersal (Bengtsson 1978; Packer 1979; Dobson 1982; Waser *et al.* 1986; Pusey 1987; Clutton-Brock 1989; Wolff 1994; Perrin & Mazalov 2000). If members of one sex disperse only to avoid inbreeding, there is no risk to the other sex and therefore theory predicts that one sex remains strictly philopatric, while the other sex (arbitrarily male or female) disperses (Gandon 1999; Perrin & Mazalov 1999). Though such a bistable equilibrium is prevented when kin competition interacts with inbreeding (unless inbreeding load is very high; Gandon 1999; Perrin & Mazalov 2000), inbreeding still makes the equilibrium more sensitive to sex

asymmetries in local competition and thereby contributes significantly to SBD (Perrin & Goudet 2001). Furthermore, inbreeding may also induce intrinsic directional biases. In polygynous species, females pay a higher cost by inbreeding since they have higher reproductive investment than males, and hence are expected to disperse more than males (Waser *et al.* 1986). This prediction is reversed if mate choice is allowed. For inbreeding load exceeding a threshold value (set by relatedness), females should prefer immigrant males, and hence boost male dispersal (Lehmann & Perrin 2003). At low inbreeding load by contrast, kin selection should induce females to prefer male relatives, and hence boost male philopatry (Lehmann & Perrin 2003). The level of inbreeding load thus appears an important issue in this context. Analytical models usually assume constant and fixed inbreeding load; however, individual-based simulations by Guillaume & Perrin (2006) show that if it is allowed to evolve, the contribution of inbreeding in driving SBD is small. Owing to strong purge and low genomic mutation rate ($U \approx 0.03$ per generation, assumed by Guillaume & Perrin 2006), large-effect deleterious mutations do not contribute significantly to dispersal pressure. Mildly deleterious mutations have higher mutation rates ($\approx 0.1 < U < 1$) but only contribute dispersal pressure if strongly recessive. Altogether, simulations show that under biologically plausible parameter values, evolutionary stable dispersal rate is increased by only one-third over the value expected from kin competition avoidance, and that inbreeding depression cannot build up at levels high enough to induce bistable sex-asymmetries in dispersal.

These conclusions might still be conservative, for example in species that have evolved alternative ways to avoid inbreeding, such as kin recognition (Lehmann & Perrin 2002; as demonstrated for example in house mice, Manning *et al.* 1992). On the one hand, kin recognition increases the potential for altruism and cooperation, promoting philopatry (with possible bias for the sex in which resource acquisition crucially depends on social bonds). On the other hand, it avoids the potential for close inbreeding, and indirectly selects for dispersal in partners of the sex that less crucially depends on social bonds (Lehmann & Perrin 2003). Such conflicting pressures are likely to induce a strong sex-bias in dispersal (Perrin & Goudet 2001).

The effects of complex social structure on dispersal deserve further formalization. Assumptions underlying analytical models typically lack a great deal of realism (Travis & French 2000). In particular, condition-dependence in dispersal strategies, documented in many empirical studies (e.g. Dieckmann *et al.* 1999; De Fraipont *et al.* 2000; Bowler & Benton 2005), is rarely incorporated. Efforts should be invested in this area, since proximate conditions determining the timing and mode of dispersal (e.g. density dependence, patterns of local kinship, aggressiveness and eviction, etc.) have the potential to shed light on its ultimate causes.

Patterns of sex-biased dispersal

While sex-biased dispersal is an almost ubiquitous feature of mammalian life history, there is enormous diversity in terms of the mode of dispersal and in the proximate causes that have been invoked to explain it (Tables 1 and 2). Even in species that are traditionally labelled philopatric (e.g. the banner-tailed kangaroo rat, Winters & Waser 2003), or those in which both sexes disperse (e.g. guanacos, Sarno *et al.* 2003), there appear to be differences between the sexes in terms of dispersal distance and rate. Dispersal rate is male-biased in the great majority of mammal species (Greenwood 1980; see Table 1 for examples) and males also appear to disperse greater distances than females (Waser 1985). It is important to note that a complete bias, where one sex remains completely philopatric while all individuals of the other sex disperse, is quite rare (e.g. white sifaka, Richard *et al.* 1993; Bechstein's bat, Kerth *et al.* 2002; ring-tailed lemur, Sussman 1992; Barbary macaque, Pusey & Packer 1987). In most species, some dispersal also occurs in the typically philopatric sex, even though the magnitude of the bias may be strong. This distinction is important for understanding the evolutionary and proximate causes of sex-biased dispersal, since as mentioned above, theory predicts that if inbreeding avoidance is the only evolutionary cause of SBD, one sex should remain completely philopatric.

Although a few empirical studies have demonstrated a difference in *dispersal distance* between the sexes (e.g. opossums, Ji *et al.* 2001; otters, Blundell *et al.* 2002; shrews, Fontanillas *et al.* 2004), information is currently quite limited. The distribution of dispersal distances should be very informative for understanding evolutionary causes of dispersal (Murrell *et al.* 2002; Rousset & Gandon 2002) because the reasons for long-distance and short-distance dispersal are likely to be very different (Ronce *et al.* 2001). Short distance dispersal is probably sufficient for avoiding inbreeding or kin competition, whereas long distance dispersal might function to colonize a new territory or escape crowding (Perrin & Goudet 2001). Dispersal distance is therefore an important avenue for future research.

The *timing* of dispersal might also provide interesting clues to ultimate causes. Although it is often assumed that individuals undergo natal dispersal as juveniles (Dobson 1982), the timing of dispersal can be quite variable, which highlights the importance of understanding the species' life history for genetic analyses (see '*Measuring sex-biased dispersal*'). Belding's ground squirrel males, for example, disperse up to 2 years *before* reaching sexual maturity (Smale *et al.* 1997), whereas male forked-marked lemurs wait 3 years *after* puberty before dispersing (Schülke 2003). Many species undergo secondary dispersal later in life, which is important to distinguish from natal dispersal,

Table 1 Examples of mammal species with male-biased dispersal

Taxonomy	Species	Common name	Mating system†	Social unit‡	Evolutionary causes§	Proximate causes¶	Hypothesis invoked for SBD**	Ref.
Primates								
Lemnidae	<i>Propithecus verreauxi</i>	White sifaka	Prom	Sm-MMU	LMC, IA	PD, EV, IhR-F	Both LMC and IA drive natal and secondary MBD. Relative importance of each determined by Mage, mating history and local demography	1,2
	<i>Lemur catta</i>	Ring-tailed lemur	Prom	Lg-MMU	LMC, IA, COOP-M	PD, IhR-F, FC	LMC, FC and IA drive MBD. M cooperate during dispersal. IhR-F promotes F philopatry	3,4
	<i>Microcebus berthae</i>	Pygmy mouse lemur	Prom	Sol	LMC		High LMC drives MBD	5
	<i>Microcebus murinus</i>	Gray mouse lemur	Prom	Sol	LMC, IA, COOP-F, LRE, IA?		Competition (M) and cooperation (F) potentially important. IA needs further investigation	6,7
	<i>Eulemur fulvus rufus</i>	Red-fronted lemur	Prom	Sm-MMU	LMC, COOP-F, LRD-F		Cooperation among related F to defend resources important determinant of F philopatry	8
	<i>Mirza coquereli</i>	Coquerel's dwarf lemur	Polyg	Sol	LMC		Benefits to F from familiarity with safe sleeping sites promotes philopatry. M able to encounter more potential mates by dispersal	9
	<i>Phaner furcifer</i>	Fork-marked lemur	Monog	M-F		EV, IhR-F	IhR-F important factor in F philopatry. M tolerated in group until adult then evicted. Very high cost to dispersal in terms of acceptance into new group	10
Cebidae	<i>Cebus apella</i>	Brown or tufted capuchin	Prom	Sm-MMU		EV	Typically MBD during aggressive takeovers but F disperse (in parallel) when LRC is high	11,12
	<i>Cebus capucinus</i>	White-faced capuchin	Prom	Lg-MMU	LMC	EV, EGA, PD	Attraction to dispersing group mates and other groups important in natal dispersal. Dispersal coalitions important for successful group takeover. Eviction of adult M after takeovers related to secondary transfer	13,14,15
	<i>Cebus olivaceus</i>	Wedge-capped capuchin	Polyg	Lg-MMU or OMU	LMC	EV	High LMC drives MBD. M evicted after group takeover	11
	<i>Saimiri sciureus</i>	Common squirrel monkey	Prom	Lg-MMU	LMC	EV	High LMC drives MBD. M evicted after group takeover	11
Cercopithecidae	<i>Macaca fuscata</i>	Japanese macaque	Polyg	Lg-MMU	IA	PD, EV, EGA	Voluntary dispersal of resident M may be in response to maturing daughters, but also attributed to overall decline in mating success after several years in group	16
	<i>Macaca sylvanus</i>	Barbary macaque	Prom	Lg-MMU	IA		IA invoked	16
	<i>Lophocebus albigena</i>	Gray-cheeked mangabey	Polyg	Lg-MMU		EGA	M attracted to other social units with oestrus F	17
	<i>Papio anubis</i>	Olive baboon	Polyg	Lg-MMU	IA, LMC	EV	IA invoked to explain natal dispersal. Secondary transfer more likely to relate to reproductive enhancement. LMC high. M evicted	18,19

Table 1 *Continued*

Taxonomy	Species	Common name	Mating system†	Social unit‡	Evolutionary causes§	Proximate causes¶	Hypothesis invoked for SBD**	Ref.
	<i>Papio cynocephalus</i>	Yellow baboon	Polyg	Lg-MMU	IA, LMC	EV, EGA	IA important. High reproductive costs for M to remaining in natal group. M evicted after losing fights with other males in group	16,20
	<i>Presbytis entellus</i>	Gray langur	Prom	Lg-MMU or OMU		EV	Eviction of maturing M drives dispersal	19,21,22
Hylobatidae	<i>Hylobates lar</i>	Common gibbon	Monog	M-F	LMC, COOP, IA		Highly cooperative species. No cost to dispersal in terms of acceptance into new group. IA, obtaining a mate and obtaining resources potentially important	23
Carnivora								
Hyaenidae	<i>Crocuta crocuta</i>	Spotted hyena	Polyg/prom	Sm-MMU		EGA, IHR-F, FC	M dispersal related to attraction of unrelated F in neighbouring groups and F mate choice. F occasionally disperse to avoid LRC	24,25
Felidae	<i>Panthera leo</i>	Lion	Polyg	Sm-MMU	IA, COOP, LRE	PD, EV	IA potentially important. M-M competition and eviction during takeovers likely proximate cause. Dispersal coalitions important for successful takeover	19
Chiroptera								
Vespertilionidae	<i>Myotis bechsteinii</i>	Bechstein's bat	Prom		IA, LMC, COOP-F, LRE		IA invoked to explain MBD because F completely philopatric and unlikely to cope with inbreeding depression	26
	<i>Nyctalus noctula</i>	Noctule bat	Polyg	Lg-OMU	LMC, LRD		Territory defence by males leads to strong LMC and variance in M reproductive success which drives MBD	27
Rodentia								
Sciuridae	<i>Spermophilus</i> sp.	Ground squirrels	Polyg/prom	Lg-MMU	COOP-F, LRE?	PD, EGA	Cooperation and LRE promotes F philopatry. M disperse in coalitions and attracted by strange extra group F	28,29,30
Cricetidae	<i>Microtus townsendii</i>	Townsend's vole	Monog/polyg*	Sm-MMU or OMU	LRE, COOP-F		Combination of cooperation between related F and LRE promotes F philopatry	31
Cetacea								
Delphinidae	<i>Tursiops aduncus</i>	Bottlenose dolphins	Prom	Lg-MMU	LMC, COOP-M,F	EV	LMC and aggression between M probably drive male dispersal	32

†Polyg, polygynous (males mate with more than one female); Monog, monogamous (males and females have only one mate at a time); Prom, promiscuous (both males and females mate successfully with different partners).

‡Sm, small; Lg, large; MMU, multimale unit; OMU, one-male unit; Sol, solitary or nongregarious; M-F, male-female pair.

§LMC, local mate competition; LRC, local resource competition; IA, inbreeding avoidance; COOP, cooperation; LRD, local resource defence, LRE, local resource enhancement.

¶PD, parallel dispersals (coalitions); EV, eviction; IHR, inheritance of rank; FC, female mate choice; EGA, extra-group attraction.

**M, males; F, females.

Ref, references: (1) Richard *et al.* 1993, (2) Lawler *et al.* 2003, (3) Pereira & Weiss 1991, (4) Sussman 1992, (5) Dammhahn & Kappeler 2005, (6) Radespiel *et al.* 2001, (7) Radespiel *et al.* 2003, (8) Wimmer & Kappeler 2002, (9) Kappeler *et al.* 2002, (10) Schülke 2003, (11) Robinson & Janson 1987, (12) Izar 2004, (13) Fedigan & Jack 2004, (14) Jack & Fedigan 2004a, (15) Jack & Fedigan 2004b, (16) Melnick & Pearl 1987, (17) Olupot & Waser 2001, (18) Packer 1979, (19) Pusey & Packer 1987, (20) Alberts & Altmann 1995, (21) Hrdy 1977, (22) Struhsaker & Leland 1987, (23) Brockelman *et al.* 1998, (24) Holekamp & Smale 1995, (25) Smale *et al.* 1997, (26) Kerth *et al.* 2002, (27) Petit *et al.* 2001, (28) Nunes *et al.* 1997, (29) Smale *et al.* 1997, (30) Devillard *et al.* 2004, (31) Lambin 1994, (32) Möller & Beheregaray 2004.

*depending on season.

Table 2 Mammal species with female-biased dispersal

Taxonomy	Species	Common name	Mating system†	Social unit	Evolutionary causes	Proximate causes‡	Hypothesis for SBD	Ref.
Eutheria								
Primates								
Lemnidae	<i>Hapalemur griseus alaotrensis</i>	Alaotrangentle lemur	Polyg (RDP)	Sm-MMU	LRD-M	EV	Benefits to M from philopatry in acquiring and defending territory. F evicted by other F	33
Atelidae	<i>Lagothrix lagotricha</i>	Woolly monkey	Prom?	Lg-MMU		EGA, FC	Home ranges overlapping. Interactions between groups common, hence familiarity with other groups important. F face low aggression if copulate early on arrival in new group	34
	<i>Ateles sp*</i>	Spider monkey	Polyg/prom	Lg-MMU	LRC	EGA, SR-F	Strong LRC promotes FBD. Sex-ratio allocation in favour of females varies with habitat. F accepted into new group easily	35
	<i>Brachyteles arachnoides</i>	Muriqui	Prom	Lg-MMU		FC, EGA	F transfer directly without aggression to new group during intergroup encounters	11,36
	<i>Alouatta seniculus</i>	Red howler monkey	Polyg	Sm-MMU or OMU	LRC, COOP	PD, EV	LRC most important factor. F reproduction in natal group limited by other F. IA unlikely since M also transfer and some F stay in natal group, also M tenure < F age at maturity. F reproductive success increased by cooperation	37,38
	<i>Alouatta palliata</i>	Mantled howler monkey	Polyg	Lg-MMU	LRC		LRC most important factor. F reproduction in natal group NOT limited by other F. M only disperse when evicted. IA unlikely as for <i>A. seniculus</i>	37
Cercopithecidae	<i>Papio hamadryas</i>	Hamadryas baboon	Polyg	Sm-OMU	COOP, IA?	EV, ABD	Philopatric M benefit from cooperation with male kin in defending F. Abduction of F by other groups also important	19,39,40,41
	<i>Colobus badius rufomitatus</i>	Red colobus	Polyand	Lg-MMU		AGG	Avoidance of aggression/infanticide from extra-group M when resident M unable to protect	19,22,42
	<i>Presbytis thomasi</i>	Thomas langurs	Polyg	Sm-OMU	IA?		IA possible as M tenure < F age at maturity. LRC low	43
Hominidae	<i>Gorilla gorilla beringei</i>	Mountain gorilla	Polyg	Sm-MMU or OMU	IA	TO, AGG	IA potentially important. Avoidance of aggression/infanticide important for timing of dispersal	19,44,45
	<i>Gorilla gorilla gorilla</i>	Western lowland gorilla	Polyg	Sm-OMU	LRC, IA	AGG, PD-F	IA potentially important. Indirect evidence for aggression avoidance. F transfer to groups with fewer F, consistent with LRC	45,46,47
	<i>Pan troglodytes</i>	Chimpanzee	Prom	Lg-MMU	LRC, IA	EGA	IA often invoked but unlikely to be sole cause. Potentially combination of LRC and IA important. F attracted to high-ranking M from other groups	18,19,48
	<i>Pan paniscus</i>	Bonobo	Prom	Lg-MMU		EGA	F attracted to high-ranking M from other groups	48
	<i>Homo sapiens**</i>	Human	Monog/(polyg/prom)	M-F (Sm-OMU)	LRE?		LRE potential factor in patrilocal societies where men inherit land and/or herds for example	49

Table 2 Continued

Taxonomy	Species	Common name	Mating system†	Social unit	Evolutionary causes	Proximate causes‡	Hypothesis for SBD	Ref.
Carnivora								
Procyonidae	<i>Potos flavus</i>	Kinkajou	Polyg/prom	Sol	LRD, COOP	IhR-M	Cooperation between M within group, inheritance of rank and LRD potential reasons for M philopatry	50
Canidae	<i>Lycaon pictus</i>	African wild dog	Monog (soc)	Sm-MMU	LRC, LRE, IA, COOP	PD, EV	Often considered an FBD species but male dispersal important in some populations. Both sexes may disperse to avoid LRC. Avoidance of inbreeding even when given opportunity supports IA	51,52,53
Chiroptera	<i>Saccopteryx bilineata</i>	White-lined bat	Polyg (RDP)	Lg-OMU	LRD		Philopatric males defend territories for breeding (LRD)	54
Insectivora								
Soricidae	<i>Crocidura russula</i>	Greater white-toothed shrew	Monog (soc)	M-F	LRC, LRD		LRC most likely explanation for FBD. Intensity of FBD dependant on spatial scale	55
Rodentia								
Cricetidae	<i>Peromyscus californicus</i>	California mouse	Monog	M-F	IA		IA invoked	56
Erthizontidae	<i>Erethizon dorsatum</i>	North American porcupine	Polyg (RDP)	Sm-OMU	IA, LRD		IA invoked because F age at first conception < M tenure. Dominant males defend breeding territories, hence benefit from philopatry	57
Perissodactyla								
Equidae	<i>Equus caballus</i>	Horse	Polyg	Lg-OMU	IA	EGA	Evidence that IA main function of FBD. F dispersal is nonrandom. F prefer to move to groups with familiar F (otherwise suffer aggression from native mares) but strange M	58
Methatheria								
Diprotodontia								
Vombatidae	<i>Vombatus ursinus</i>	Common wombat	Polyg***	Sol	LRD, COOP	TB	LRD and cooperative behaviour by related M in close burrows potentially explains male philopatry	59,60

Legend as for Table 4 except:

†RDP, resource defence polygyny; Polyand, polyandrous (females mate with more than one male).

‡ABD abduction, SR sex-ratio allocation (a female-biased sex ratio is predicted to favour FBD), TB territory bequeathal to offspring by breeding females.

Ref, references: (33) Mutschler *et al.* 2000, (34) Nishimura 2003, (35) McFarland Symington 1987, (36) Strier & Ziegler 2000, (37) Crockett & Eisenberg 1987, (38) Pope 2000, (39) Kummer 1968, (40) Stambach 1987, (41) Hammond *et al.* 2006, (42) Marsh 1979, (43) Sterck 1997, 1998, (44) Harcourt *et al.* 1976, (45) Stokes *et al.* 2003, (46) Stewart & Harcourt 1987, (47) Bradley *et al.* 2004, (48) Nishida & Hasegawa 1987, (49) Wilkins & Marlowe 2006 (review, see text for examples), (50) Kays *et al.* 2000, (51) Frame & Frame 1976, (52) Malcolm & Marten 1982, (53) McNutt 1996, (54) Bradbury & Vehrencamp 1976, 1977, (55) Favre *et al.* 1997, (56) Ribble 1992, (57) Sweitzer & Berger 1998, (58) Monard & Duncan 1996, (59) Banks *et al.* 2002, (60) Skerratt *et al.* 2004.

**Ateles* sp. *A. belzebuth*, *A. fusciceps*, *A. geoffroyi*, *A. paniscus*. Note these species are 'potentially polygynous' but females are also promiscuous.

**Intraspecific variation is found in humans in terms of sex-biased dispersal, mating and social system. See main text for more details.

***In this case both males and females mate successfully with different partners, but males have higher variance in reproductive success (Ref. 59).

since it is likely to be motivated by very different reasons. For example, there is good evidence that close inbreeding avoidance is an important driving force behind natal male dispersal in olive baboons, but secondary dispersal (by about a quarter of all males) is more likely to result from aggressive eviction, which seems to be a more important determinant of secondary transfer than natal dispersal (Packer 1979).

Proximate causes of sex-biased dispersal

Eviction, attraction to members of other groups, and benefits of group dispersal are among the most important proximate explanations for sex-biased dispersal (Tables 1 and 2). Whereas emigration seems voluntary in most species, forceful *eviction* has been documented in some cases, and as mentioned above, is a potentially important reason for secondary transfer. Eviction is often the result of aggression from adult males in response to increasing maturity of male adolescents (e.g. howler monkey, grey langur, gibbon, Table 1) but is also a consequence of group takeover (e.g. white-faced capuchin, Jack & Fedigan 2004; Table 1). While aggressiveness leading to eviction is more common among males, it has also been documented among females, particularly if low-ranking (e.g. chimpanzees, Pusey & Packer 1987; Table 2, spotted hyenas, Holekamp & Smale 1995; Smale *et al.* 1997; Table 1). While intrasex eviction points to competition for mates (in males) or resources (in females), intersex eviction (e.g. in white-footed mice, Wolff 1992; several macaque species, Packer & Pusey 1987) invokes inbreeding avoidance as the most likely ultimate cause.

Attraction to sexual partners outside the natal group is a potentially important trigger of dispersal, which is independent of social structure. *Extra-group attraction* has been shown to drive emigration in several group-living primate species such as chimpanzees, macaques, mangabeys, vervets and guenons (Pusey & Packer 1987; Olupot & Waser 2001; Jack & Fedigan 2004a; Tables 1 and 2). In this case, the timing of dispersal generally coincides with the mating season. Emigration occurs at sexual maturity and clusters around the peak breeding season, suggesting male sexual attraction to extra-group females (Jack & Fedigan 2004a). Olive baboon males, for example, are attracted to oestrus females in neighbouring groups and females may solicit the attention of potential dispersers (Packer 1979). In grey-cheeked mangabeys, spatio-temporal availability of oestrus females is a major proximate factor influencing transfer, and males show a greater tendency to move into new groups that contain higher numbers of oestrus females than their previous group (Olupot & Waser 2001). Generally though, males are not necessarily attracted to groups with many females but rather to groups containing unfamiliar females (Pusey & Packer 1987).

If there is cooperation between relatives (for example in acquisition of resources or in raising young), there are clear benefits to individuals by remaining philopatric. Under these circumstances, cooperation is likely to oppose dispersal. However, this cost can be circumvented if individuals disperse as a group. *Parallel dispersal* maintains coalitions and familiar relationships for dispersing individuals. Although most mammals tend to disperse individually, parallel dispersal is known in some species (Tables 1 and 2). Dispersing in a coalition may be of particular benefit to immature males in aiding initial entry into a foreign group. In lions for example, coalitions of related males from the same cohort leave the natal group together (Pusey & Packer 1987). Coalitions are more successful at taking over new prides and there are clearly inclusive fitness benefits to subordinate males by dispersing with dominant kin (Pusey & Packer 1987). In white-faced capuchins, 82% of male transfers take place in the company of older maternal siblings or members of the same age cohort, which are likely to be close relatives (Jack & Fedigan 2004a). However, group dispersal might sometimes occur simply because the limited duration of female oestrus influences the period when transfer occurs (e.g. macaques, Melnick & Pearl 1987).

Is sex-biased dispersal linked to social complexity?

An increase in the magnitude of sex-biased dispersal with increased social complexity (i.e. the degree of sociality and communicative complexity) is expected on theoretical grounds, from the interaction between the benefits of kin cooperation and the costs of inbreeding (Perrin & Goudet 2001). Greenwood (1980) noticed that the degree of sociality influences the magnitude of the sex bias in dispersal, and sex differences are indeed particularly striking among long-lived, highly social, polygynous mammals (Pusey 1987; Smale *et al.* 1997). Moreover, there is also a close link between sex-biased dispersal and social organization in birds (especially communal breeders, e.g. Florida scrub jay, Greenwood & Harvey 1982). In line with prediction, Devillard *et al.* (2004) found an increase in the magnitude of male-biased dispersal with increasing social complexity in polygynous ground dwelling sciurids (ground squirrels, marmots and prairie dogs). The increased bias, however, was determined solely by an increased male dispersal, and not, as also expected, by a concomitant decreased female dispersal (Perrin & Goudet 2001). Unfortunately, levels of polygyny and sociality are linked, so the correlation between male dispersal rate and social complexity is probably confounded by a mating system effect (Devillard *et al.* 2004). This important question therefore warrants investigation in other species groups to address the effect of mating system and to establish whether this is a phylogenetically independent pattern.

Exceptions to the rule: female-biased dispersal in mammals

Although female-biased dispersal is rare in mammals (Greenwood 1980), it is found in phylogenetically diverse taxonomic groups, with varying social structures and mating systems, suggesting a wide range of evolutionary and proximate explanations. As is often the case in evolutionary biology, studying the exceptions to a rule can provide unique insights into more general explanations, and we therefore address the patterns and causes of female-biased dispersal in some detail. In Table 2 we provide a summary of all mammal species with FBD for which there is good data available. Inspection of Tables 1 and 2 together reveals four general points.

First, in some cases, several closely related species all exhibit FBD (e.g. Atelidae, Hominidae, Table 2). More often though, both FBD and MBD can be found in groups of closely related species with apparently similar life histories, and in some cases there is phylogenetic evidence that FBD has evolved independently from the ancestral state of MBD (e.g. hamadryas baboons, Hammond *et al.* 2006). Second, although mating system is often considered to be a good predictor of direction of SBD, dispersal is male-biased in several monogamous species (Table 1), and several polygynous species have predominantly female dispersal (Table 2), suggesting that the hypothesis of Greenwood (1980) is too simplistic. Third, several species that live in one male units (OMUs), which are known to have high local mate competition, exhibit FBD (e.g. hamadryas baboons, gorillas, horses). These first three points illustrate the enormous diversity in terms of taxonomy, mating system, social unit and the direction of sex-biased dispersal. Finally, there appears to be an overrepresentation of primates with FBD compared to other mammal groups, but it is unclear whether this reflects the disproportionate investment in field studies of these species (highlighted by the high representation of primate species in both Tables 1 and 2), and good quality data is needed from other taxonomic groups to investigate this.

In terms of evolutionary explanations for female-biased dispersal, FBD makes intuitive sense in species with resource defence systems, where males take the leading role in acquisition and defence of resources and there are considerable benefits to males by remaining philopatric. This strategy is quite common in pair-breeding birds (Greenwood 1980), and the same logic could account for FBD in pair-breeding mammals, such as the greater white-toothed shrew, in which males take a major role in territory acquisition and defence (Favre *et al.* 1997; Bouteiller-Reuter & Perrin 2005). However, resource defence may also account for FBD in some polygynous mammals (in which case the mating system is termed 'resource defence polygyny'), such as the white-lined bat, Alaotran gentle

lemur and North American porcupine (Table 2). In FBD species with high local mate competition, both inbreeding avoidance and cooperation certainly play a role. First, when dominant males have long tenure in their social groups (be they OMUs or multimale units, MMUs, Tables 1 and 2), their daughters disperse on approaching sexual maturity to avoid mating with their potential father (e.g. gorillas, hamadryas baboons, chimpanzees, howler monkeys, African wild dogs, Clutton-Brock 1989). Second (and not exclusively), males may benefit from kin cooperation and form coalitions to prevent extra-group males gaining access to females. In both OMU and MMU species, the advantages to an individual male from kin-cooperation may sometimes outweigh those of dispersal and promote male philopatry. Cooperation among male kin for territory acquisition and mate attraction might be important in mammal species that form 'dispersed male networks' to defend females (e.g. western gorillas, Bradley *et al.* 2004; possibly hamadryas baboons, Hammond *et al.* 2006). Finally, local resource competition has been invoked to explain several cases of FBD, even in polygynous species where LMC is expected to be greater than LRC (Table 2). This is highlighted by spider monkeys, in which female dispersal is driven by a combination of sex-ratio bias in favour of females and LRC between females, which are directly related to habitat pressures (McFarland Symington 1987).

Several proximate causes are also important to consider when attempting to explain female-biased dispersal. Extra-group attraction, aggression avoidance, eviction and benefits of parallel dispersal are important determinants of FBD as well as MBD (Tables 1 and 2). Another important consideration is that the cost of immigration might be less for females than for males, since they are more readily accepted into a new group (e.g. spider monkeys, muriquis, hamadryas baboons, Table 2), particularly if they copulate early on arrival into their new group (e.g. woolly monkey, Table 2). An extra explanation that is probably specific to females is that of abduction by males from outside the group during aggressive encounters (e.g. hamadryas baboons, Table 2). Post-weaning territory bequeathal to offspring has been invoked to explain female dispersal in species where juveniles need to acquire a key resource such as a burrow to survive. Bequeathal involves active, strategic dispersal by breeding females and appears to be condition-dependent (Price & Boutin 1993). Since adult females may be able to obtain this resource more easily than juveniles, territory bequeathal may increase the female's fitness. However, most of the species in which bequeathal has been observed have male-biased dispersal (e.g. red squirrels, Price & Boutin 1993; Berteaux & Boutin 2000, hairy-nosed wombat, Johnson & Crossman 1991; Columbian ground squirrels, Harris & Murie 1984, except common wombat, Banks *et al.* 2002; which has FBD, Table 2), so this cannot be taken as a general explanation for FBD.

Finally, it has also been argued that females transfer to avoid infanticidal males (Marsh 1979; Stokes *et al.* 2003), but there appears to be very little direct evidence supporting prevalence of infanticide in FBD species (except for red colobus monkeys, mountain gorillas, and Thomas's langurs, Table 2). We would argue that it seems even more risky a strategy to attempt to immigrate into a new group with an infant who has not been sired by a resident male, or to emigrate following the death of an infant as a direct result of a male takeover (e.g. Stokes *et al.* 2003), and therefore this explanation seems an unlikely general explanation for FBD.

What about humans?

Far too often, there is a gap between studies of dispersal patterns in humans and those of other mammals, while in fact humans provide an important example for the occurrence of intraspecific variation in sex-biased dispersal (e.g. Hamilton *et al.* 2005a), and highlight the importance of geographical scale on dispersal patterns. We therefore believe a discussion of human patterns of sex-biased dispersal is justified here.

The conflicting results from the many papers describing sex-biased dispersal patterns in humans can be rather bewildering. The first global comparison of mitochondrial DNA (mtDNA) and Y chromosome patterns indicated a much higher migration rate for females than for males (Seielstad *et al.* 1998). By contrast, a more recent study, also on a global scale, found no evidence for sex-biased dispersal (Wilder *et al.* 2004), although reasons for this discrepancy could be methodological differences such as sampling strategy (the samples used in the Wilder study came from sparsely distributed populations). At a regional level, patterns can usually be explained by cultural differences or known historical events. Consistent with Seielstad *et al.* (1998), the majority of regional-scale studies have reported female-biased dispersal, which is typically associated with patrilocality (Perez-Lazaun *et al.* 1999; Oota *et al.* 2001; Bolnick *et al.* 2006). Patrilocality and female-biased dispersal is much more common in pastoral communities, where males who inherit their father's land and herds tend to be more successful in attracting a wife (Wilkins & Marlowe 2006), than in hunter-gatherer societies, where resource accumulation is less important (Destro-Bisol *et al.* 2004; Wood *et al.* 2005). One interesting related point is that a shift to patrilocal societies and female-biased dispersal may have occurred since the agricultural revolution, which started approximately 10 000 years ago, since modern hunter-gatherers (which are often seen as models for pre-agricultural societies) are characterized by similar patterns of male and female dispersal or occasionally male-biased dispersal (Wilkins & Marlowe 2006). The relationship between patrilocality and female-biased dispersal is however, not apparent in highly endogamous patrilocal populations

from the Indian subcontinent, which questions the universality of this hypothesis (Kumar *et al.* 2006). Male-biased dispersal has been documented in connection to matrilocality (Bolnick *et al.* 2006), which is rare in human societies compared to patrilocality, and immigration seems to be much less regulated in matrilocal compared to patrilocal populations (Hamilton *et al.* 2005a). MBD tends to be more associated with historical events than with cultural practices, for example the introgression of European Y chromosomes, but not mtDNA, in the Americas post 1492 (Mesa *et al.* 2000; Seielstad 2000; Bolnick *et al.* 2006; see Bosch *et al.* 2003; Al-Zahery *et al.* 2003 for examples from other regions).

An important outcome from recent studies of human dispersal is that patterns seen at the local scale may not reflect those at a larger geographical scale (Kumar *et al.* 2006), and that large geographical scale patterns are likely to be representative of long-term demographic processes, whereas local-scale patterns detect events in the recent history of that region (Wilkins & Marlowe 2006). This could have important implications for studies of natural populations that wish to determine if the relative rates of male and female migration have changed over time, for example in response to climatic events, habitat fragmentation or anthropomorphic factors.

Measuring sex-biased dispersal

Our ability to detect, quantify and interpret sex-biased dispersal will depend on the choice of appropriate methods to study its occurrence in natural populations. Ideally, a combination of both field observations and genetic methods is required to obtain a comprehensive picture of dispersal patterns and to make inferences about the proximate and ultimate causes for SBD. Field data provide valuable insights into the species' social and reproductive behaviour, which are essential to better understand the potential reasons for SBD, but they do not always allow quantification of how dispersal translates into gene flow, since effective dispersal can be low even when there is high mobility (Gandon 1999). Moreover, for species that are particularly vagile, difficult to individually identify or to mark and recapture, estimating sex-biased dispersal by direct observation is not always feasible. Genetic methods can be used to complement and reduce the invasiveness, effort and expense of mark-recapture studies and give insights into how dispersal translates into effective dispersal and gene flow. An appreciation of the species' life history is essential, at the very least to establish when dispersal is likely to occur. As a guideline, many species undergo natal dispersal before maturity (but see '*Patterns of sex-biased dispersal*'). Sampling juveniles therefore provides access to predispersal individuals, while sampling adults provides a mixture of residents and immigrants. It is important to emphasize that these different

Box 1 The hierarchical island model

Assumptions and application of the island model:

To understand how dispersal can be measured, it is important to consider dispersal in a population genetics framework. The simplest approach is to imagine an island model of populations (Wright 1931). Each deme has N individuals, and a proportion, m , of the individuals are immigrants. Under migration-drift equilibrium, F_{ST} provides an indirect measure of migration in the form, $N_e m$ (where N_e is the effective size of the deme, subpopulation or population, and m is the number of immigrants) from Wright's (1943) formula for a diploid locus:

$$\hat{F}_{ST} \approx \frac{1}{4N_e m + 1} \quad (1)$$

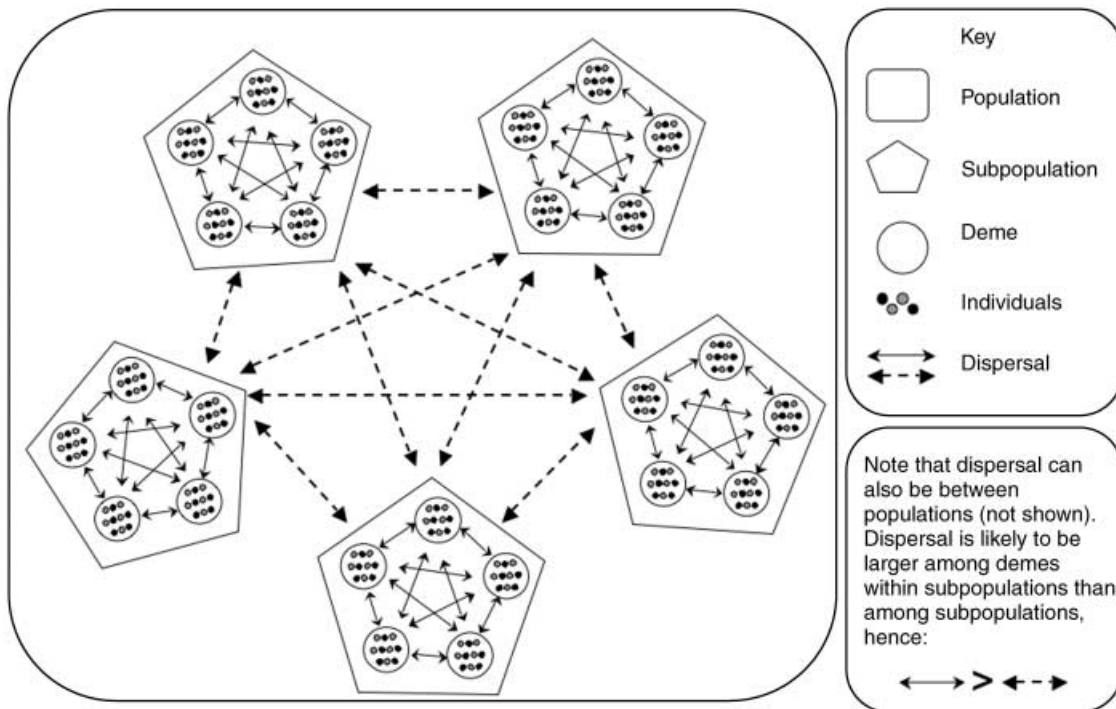
Access to sex-specific markers enables us to expand this approach to investigate sex-specific gene flow. Different functions of male and female dispersal rate and

effective population sizes are substituted in equation 1, depending on the marker considered (Table 3).

Unfortunately there are several assumptions to the island model that are rarely met in practice, so any estimation of $N_e m$ by this method should be interpreted with great care (see Whitlock & McCauley 1999 for a detailed argument of this, and Balloux & Lugon-Moulin 2002 for a discussion on the limitations of F_{ST} for estimating $N_e m$). The assumptions are:

- 1 All populations are stable in size
- 2 All populations have $N_e m$ individuals arriving as migrants per generation
- 3 Migration is random with respect to distance (in other words there is no isolation by distance)

However, if we assume that the assumptions apply equally to both sexes (which is probably fair, except perhaps for assumption 3), relative estimates of F_{ST} can be useful to compare the number of migrant males and females, and hence to measure the direction of sex-biased dispersal.



cohorts should be analysed separately. Doing otherwise would not only reduce the ability of tests to detect SBD (Prugnolle & de Meeûs 2002), but also lose the opportunity to gain insightful information from the contrast between pre- and post-dispersal samples (see below).

Conventional genetic methods for measuring direction of SBD have been previously classified into those that measure sex-biased gene flow, or instantaneous dispersal (Prugnolle & de Meeûs 2002). Both of these approaches assume a classical island model of populations (Box 1),

Table 3 Effective population size (N_e) and dispersal rate (m) to be used for different genomic regions in equation 1 (Box 1) as functions of male and female effective sizes and dispersal rates

	N_e	m
Autosomal markers	$\frac{4N_m N_f}{N_m + N_f}$	$\frac{m_m + m_f}{2}$
X chromosome	$\frac{9N_m N_f}{4N_m + 2N_f}$	$\frac{m_m + 2m_f}{3}$
Y chromosome	$\frac{N_m}{2}$	m_m
mtDNA	$\frac{N_f}{2}$	m_f

and a simple population genetics framework. The simplest approach builds on Wright's (1943) formula for genetic differentiation between subpopulations (equation 1, Box 1), which provides us with an indirect measure of the effective dispersal rate. Although F_{ST} offers only an approximate solution (since it relies on simplistic assumptions, Whitlock & McCauley 1999; Box 1), even though underlying assumptions of the island model (and hence summary statistics that assume it, such as F_{ST} and relatedness) are unrealistic in many situations, this does not affect the relative estimates of male and female migration rates.

Sex-biased gene flow

Direction of sex-biased gene flow can be measured using sex-specific markers, i.e. maternally inherited mtDNA or the paternally inherited nonrecombining region of the Y chromosome (NRY). Since these markers are nonrecombining, information on historical patterns of gene flow is maintained in successive generations. Sex-biased gene flow can be inferred most simply through patterns of haplotype distribution (e.g. Eriksson *et al.* 2006), or from the relative estimate of gene flow in males compared to females obtained by calculating F_{STY} and $F_{STmtDNA}$ (e.g. Hammond *et al.* 2006). This can be estimated assuming an effective population size (N_e) of Y-chromosomes and mtDNA one-quarter that of the autosomes (due to copy number differences alone, Box 1 and Table 3). In addition, the parameter $N_e v = (1/F_{ST}) - 1$, where v incorporates mutation (μ) and migration (m) ($v = m + \mu - m\mu$) has been used several times to estimate the relative effective population size and/or rate of gene flow from sex-specific markers (Seilestad *et al.* 1998; Destro-Bisol *et al.* 2004; Eriksson *et al.* 2006). A high ratio of $N_e v_{mt}/N_e v_Y$, such as that recently found in bonobos ($N_e v_{mt}/N_e v_Y = 282$, Eriksson *et al.* 2006) indicates a much higher effective size for females and/or rate of gene flow, and a ratio greater than one has been described in several human populations (e.g. Seilestad *et al.* 1998; Destro-Bisol *et al.* 2004).

It is important to stress that difference in F_{ST} between Y and mtDNA may stem from differences in male and female effective population size as well as dispersal rate. In hamadryas baboons for instance, female-biased dispersal combines with a highly polygynous mating system and a female-biased adult sex ratio to generate a particularly small male N_e and a strong contrast in F_{ST} between Y and mtDNA ($F_{STY} \ll F_{STmtDNA}$, Hammond *et al.* 2006). Fortunately, Chesser & Baker (1996) and Laporte & Charlesworth (2002) provide joint analyses of the combined effects of dispersal patterns and mating systems on the effective population size and population structures for sex-specific markers, which provide informative guidelines for interpreting patterns. Other caveats also apply though when analysing gene flow using sex-specific markers. First, a large sampling variance is associated with Y and mtDNA markers owing to their lack of recombination, so differences may be simply stochastic. Second, there can be a large difference in the mutation rate between these loci, depending on the type of marker selected, and this needs to be considered. Finally, this method obviously relies on characterizing informative sex-specific markers, and relative lack of variability on the Y chromosome may be a limiting factor here (Hellborg & Ellegren 2004; Hammond *et al.* 2006; Lawson Handley *et al.* 2006a,b). However, the increasing availability of Y-linked markers (Hellborg & Ellegren 2003), particularly microsatellites (Erler *et al.* 2004; Lawson Handley & Perrin 2006) will hopefully facilitate its future use in this type of study.

Instantaneous dispersal

Recombining biparental markers (such as autosomal microsatellites) measure sex-biased dispersal in one generation since parental alleles are independently assorted in the offspring. Relative estimates of F_{ST} for post-dispersal males and females can therefore be used to measure the direction of sex-biased instantaneous dispersal (e.g. Goudet *et al.* 2002; Prugnolle & de Meeûs 2002; Hammond *et al.* 2006), whereas dispersal rates can be quantified by contrasting adults and predispersal juveniles (Vitalis 2002; Fontanillas *et al.* 2004).

Standard statistical tests for measuring the direction of instantaneous SBD are based on population-level genetic structure of males and females (F_{IS} , F_{ST} or relatedness r , Weir & Cockerham 1984; Whitlock & McCauley 1999; Goudet *et al.* 2002) or the probability of an individual's assignment to a population (mean and variance of the corrected assignment index, $mAIC$ and $vAIC$, respectively, Paetkau *et al.* 1995; Favre *et al.* 1997; Waser & Strobeck 1998; Goudet *et al.* 2002). The logic and predictions of these standard tests are detailed in Table 4. The power to detect sex-biased dispersal by these methods depends on the intensity of the bias and on the rate of dispersal (Goudet *et al.* 2002). If only one sex disperses, then the bias is normally detectable by

Table 4 Logic and predictions of statistical tests for sex-biased dispersal

Statistic	Definition	Logic	Prediction			References
			Pre-dispersal	MBD	FBD	
F_{IS}	Measure of inbreeding within subpopulations relative to the total	Expect higher F_{IS} and heterozygote deficit in the dispersing sex due to Wahlund effect, since individuals sampled from a single patch will be a mixture of residents and immigrants	$F = M$	$F < M$	$F > M$	1,2,11
F_{ST}	Genetic differentiation among subpopulations	Expect philopatric sex to exhibit higher F_{ST} than dispersing sex	$F = M$	$F > M$	$F < M$	1,2,3,4,11
Relatedness (r)	Degree of relatedness among individuals within subpopulations	Expect individuals living in close proximity to be more related on average than individuals taken from the whole population. Individuals of the philopatric sex will have higher r than those of the dispersing sex	$F = M$	$F > M$	$F < M$	2,7,8,9,10,11
Mean corrected assignment index ($mAlc$)	The mean probability of assignment of an individual to a population	A positive Alc value indicates that the genotype is more likely to come from the sampled population. An individual with a negative Alc value is more likely to be an immigrant. $mAlc$ will be lower in the dispersing sex.	$F = M$	$F > M$	$F < M$	2,3,5,6,11
Variance of corrected assignment index ($vAlc$)	The variance in the probability of assignment of an individual to a population	As above, but $vAlc$ will be larger in the dispersing sex because they are expected to be a mixture of residents and immigrants.	$F = M$	$F < M$	$F > M$	2,3,5,6,11

References: (1) Weir & Cockerham 1984, (2) Goudet *et al.* 2002, (3) Prugnolle & de Mees 2002, (4) Mossman & Waser 1999, (5) Paetkau *et al.* 1995, (6) Favre *et al.* 1997, (7) Ishibashi *et al.* 1997, (8) Piertney *et al.* 1998, (9) Knight *et al.* 1999, (10) Surridge *et al.* 1999, (11) Hammond *et al.* 2006. Predictions of test statistics based on a predispersal sample of males and females (representing a null control), and populations of postdispersal male and female adults, under a hypothesis of male-biased dispersal (MBD) or female-biased dispersal (FBD).

any of the methods described here, so long as sampling is intensive (i.e. many individuals from many populations), but only F_{ST} and $mAlc$ retain enough power when the bias intensity drops to 80:20. When dispersal rate is high, a population will consist of a large proportion of immigrants, and populations are less differentiated as a result. When dispersal rate is very low, immigrants constitute only a small proportion of the individuals sampled and may not be detected at all. Not surprising perhaps then that the maximal power for all tests is achieved when dispersal rate is at an intermediate value (approximately 10% per generation), but some tests perform better than others under different rates of dispersal. $vAlc$ is particularly sensitive to rare alleles, whereas F_{ST} is more sensitive if dispersers constitute a larger proportion of the sample, and $mAlc$ is somewhere in between these two. When dispersal is lower than 10% per generation, $vAlc$ outperforms the other statistics, whereas F_{ST} is more robust in terms of bias intensity and sampling regime (Goudet *et al.* 2002).

It is essential to keep in mind the relative power (or lack of power) of these tests when designing experiments, since sampling design and choice of number and variability of loci can influence the possibility to detect SBD. Simulation experiments have shown that it is better to increase the number of individuals per population rather than the number of populations sampled (Goudet *et al.* 2002). This makes intuitive sense because with more individuals per population, there is more opportunity for sampling immigrant genotypes and allele frequencies are better estimated, and therefore, immigrant and resident genotypes can be more readily distinguished. The power of certain statistics (F_{ST} , r , $mAlc$ and $vAlc$) to detect SBD can be improved by increasing the number of polymorphic loci, but no significant gain is expected above 20 polymorphic microsatellites, and Goudet *et al.* (2002) caution that it is better to invest in the number of individuals rather than the number of loci. It may seem that the lack of power to detect SBD using these statistics is restrictive, but the growing number of case studies that have employed these methods and successfully detected SBD would suggest that bias intensity is often sufficiently high in practice.

Although the summary statistics described above can be informative for estimating the direction of SBD, they cannot be relied upon to provide quantitative estimates of dispersal rates (unless estimates are compared before and after dispersal, see below) since any summary statistic represents a population 'average' as far as genotypes are concerned.

Towards more quantitative estimates of sex-biased dispersal

While the direction of mammalian sex-biased dispersal, which is comparatively easy to establish, appears to strongly

favour males, the magnitude and intensity of the bias are more difficult to measure and vary greatly between species and even within the same species. Recent advances in statistical approaches mean that quantitative estimates of sex-biased dispersal rate can be more readily obtained. Vitalis (2002) showed that, assuming an island model of dispersal (Box 1), the ratio of sex-specific F_{ST} estimated after dispersal over F_{ST} estimated before dispersal is a simple function of the sex-specific dispersal rate. This function estimates the proportion of immigrant individuals in a subpopulation per generation, a parameter that includes differential dispersal costs to the sexes (Vitalis 2002).

The selective pressures on dispersal are likely to depend on the spatial scale considered (Ronce *et al.* 2001), and so far, few studies have considered that dispersal bias might vary with geographical scale. In one example, fine-scale variation in SBD was detected in the Australian bush rat using spatial autocorrelation analyses, illustrating the

potential for this type of analysis to measure variation in dispersal with spatial scale (Peakall *et al.* 2003). Fontanillas *et al.* (2004) extended the Vitalis (2002) approach to account for the hierarchical structure of populations. An application to the greater white-toothed shrew showed that dispersal was significantly female-biased at the breeding group level, but not at the among population level. Moreover, the total dispersal rate of females was almost four times higher than that of males, but when broken down into local and larger geographical scales the authors noted that the male dispersers were travelling further than the females, so that among villages, dispersal was no longer female biased. Individual-based simulations showed that, to compare spatial scales, sampling should include the highest hierarchical level at which dispersal is thought to occur, the number of groups per population should approximate the number of populations in the sample, and sampling should be as exhaustive as possible within groups

Box 2 Glossary and Abbreviations

Dispersal: movement of individuals from one group, deme, subpopulation or population to another in which they successfully breed (thus resulting in potential changes in allele frequencies). Also referred to as '**effective dispersal**' (as opposed to ecological dispersal which is simply the movement of an individual from one place to another). Unless stated otherwise (e.g. under secondary transfer), we consider dispersal as emigration from the natal group.

Female-defence polygyny: mating system in which a dominant male defends mating access to a harem of several females (common in mammals).

Gene flow: dispersal followed by successful reproduction. In this review we use the term 'gene flow' to refer to historical patterns maintained in successive generations (as opposed to 'instantaneous dispersal').

Inclusive fitness benefits: an expansion of the concept of 'fitness' to include benefits accrued to relatives. Since relatives share their genetic material an apparently altruistic act toward a relative may in fact enhance the inclusive fitness of the individual performing the act.

Inbreeding avoidance (IA): avoidance of mating with closely related individuals.

Inbreeding depression: decline in fitness due to breeding with close relatives.

Inbreeding load: a function of the number of deleterious alleles in a population (i.e. the genetic load) governed by the deleterious mutation rate (U) as well as selection and dominance coefficients.

Instantaneous dispersal: dispersal in one generation. Measured using biparentally inherited, recombining markers since parental alleles are independently assorted in the offspring.

Kin selection: the concept that an individual gains inclusive fitness benefits by enhancing the reproduction of relatives (Hamilton 1964).

Local mate competition (LMC): competition for mates among related, same-sex individuals. Typical among males in polygynous mammals.

Local resource competition (LRC): competition for resources among related individuals. Typical among males in species with resource-defence monogamy.

Local resource enhancement (LRE): the benefits gained from local interactions with relatives.

Patrilocality: the tendency in human populations for a wife to move into her husband's natal household (opposite: matrilocality).

Philopatric: an individual that remains in its natal group to breed (i.e. does not undergo dispersal).

Resource-defence monogamy: monogamous mating system in which males take the leading role in acquisition and defence of resources (common in pair-breeding birds).

Secondary transfer: dispersal after initial departure from natal group, for reasons potentially very different to natal dispersal (e.g. eviction after group takeover).

Other abbreviations used:

SBD, sex-biased dispersal

MBD, male-biased dispersal

FBD, female-biased dispersal

OMU, one-male unit

MMU, multiple unit

(Fontanillas *et al.* 2004). One should also consider that if the scale over which dispersal is measured is smaller than the scale over which organisms actually move, then average dispersal distances can be grossly underestimated (the so called 'right censoring problem', Dieckmann *et al.* 1999).

Individual-based assignment tests based on likelihood (e.g. Waser & Strobeck 1998) or Bayesian principles (e.g. Pritchard *et al.* 2000) offer several advantages over summary statistics and should be more powerful because they do not average over the population, allow immigrant individuals to be readily identified, are more geographically explicit, and in the latter do not require populations to be predefined (see Manel *et al.* 2005 for a review). Although individual assignment techniques based on Bayesian principles applied to multilocus genotypes are becoming standard tools in molecular ecology (Manel *et al.* 2005), their potential for studying dispersal has perhaps yet to be realized (but see Fraser *et al.* 2004; Natoli *et al.* 2005; for exceptions). They do, however, provide a particularly interesting and powerful alternative to the moment-based methods that underlie the statistical inferences mentioned above (Beaumont & Rannala 2004). The accuracy of partial Bayesian (Rannala & Mountain 1997; Cornuet *et al.* 1999; implemented in the software GENECLASS) and fully Bayesian (Pritchard *et al.* 2000 implemented in STRUCTURE) methods of individual-based assignment to measure dispersal was recently assessed by comparing microsatellite data to long-term mark-recapture records in the grand skink (Berry *et al.* 2004). Encouragingly, similar estimates of the proportion of dispersing individuals were obtained and assignment tests correctly identified the natal population of 65–100% of individuals even when dispersal was quite common (5–20% of the population consisted of dispersers). Moreover, assignment tests provided a qualitative idea of the scale of dispersal and quantitative estimates of the number of dispersers, which in both cases was comparable to estimates obtained from mark-recapture studies (Berry *et al.* 2004). These methods could be extended to studies of SBD by simply comparing males and females separately.

Developments in Bayesian (or partial Bayesian) methods also have relevance for studying sex-biased dispersal rates. The principle of this approach is to compare summary statistics (in this case, e.g. nucleotide diversity for sequence data or heterozygosity for microsatellite data) from observed data with those simulated under a model for which the parameters are known (Beaumont *et al.* 2002). Since models of any complexity can in theory be simulated, those that more closely reflect biological reality can be estimated. Recently, approximate Bayesian methods were used to compare differences in male and female dispersal levels in natural populations of the common vole (Hamilton *et al.* 2005b). An extreme sex bias in dispersal was found, with males dispersing at ~20 times the rate of females. The authors caution though that this method could overestimate the

effective number of migrants if there is a large discrepancy in dispersal distance between sexes (Hamilton *et al.* 2005b). Interestingly, this approach could be used to compare autosomal microsatellites and mtDNA data to obtain estimates of male dispersal, bypassing the need for male-specific markers (Hamilton *et al.* 2005b).

Conclusions and prospects

The recent rise of molecular tools has helped to document empirical patterns of dispersal, confirming that SBD is widespread among mammals, and varies widely in direction and intensity. The evolutionary causes behind these patterns though still require much clarification. The main emerging insight relates to the crucial role of social systems, but the complex interactions between inbreeding avoidance, kin competition and cooperation makes the building of a theoretical framework able to account for the impressive diversity of patterns difficult.

From this review, a few directions can be identified from which new insights would be particularly welcome. First, concerning evolutionary modelling, efforts are needed to incorporate the subtleties of social interactions, since social life turns out to play a crucial role in promoting sex-bias in dispersal. More emphasis should also be put on the incorporation of condition dependence of sex-specific dispersal, which might gain crucial importance when interpreting observed patterns in terms of evolutionary causes. On the empirical front, progress is expected from the development of male-specific markers (Y chromosome), from investigations on sex differences in dispersal distances, and from the delineation of condition dependence in dispersal (modes and proximate causes). There is a real need to properly integrate genetic information and careful observational data, since the two approaches provide complementary information (e.g. on proximate causes and effectiveness of gene flow) required for any interpretation in evolutionary terms. For instance, only observational data will be able to disentangle emigration from immigration and evaluate dispersal costs. It is also worth considering that sex-biased dispersal may result from differences in emigration rate or in dispersal mortality (e.g. Waser *et al.* 1994), and hence stem from very different evolutionary causes. The separation of dispersal into its component stages (emigration, interpatch movement and immigration), which involve very different decisions, is still rarely taken into account in empirical studies (Bowler & Benton 2005). Intraspecific variation in sex-biased dispersal is clearly important in humans (see above), has been demonstrated in other mammals (e.g. shrews, Fontanillas *et al.* 2004), and is an essential avenue for further research, to explore the effects of varying ecology and demography on dispersal. Data analysis and statistical treatments will gain from the spread and implementation of Bayesian approaches, which allow

more realism in the scenarios to be tested. Bayesian methods of individual assignment, for instance, may allow some freedom from the constraints of predefining populations (see general review in Manel *et al.* 2005).

Sex-biased dispersal has been confirmed in other taxonomic groups including birds (Cooke *et al.* 1975; Greenwood 1980; Clarke *et al.* 1997; Scribner *et al.* 2001; Hansson *et al.* 2003; Wright *et al.* 2005), fish (Knight *et al.* 1999; Pardini *et al.* 2001; Hutchings & Gerber 2002; Taylor *et al.* 2003; Bekkevold *et al.* 2004), and amphibians (Austin *et al.* 2003; Palo *et al.* 2004). However, as reflected in this review, there has been a disproportionate investment in studies of SBD in mammal compared to nonmammal species. It will be important to overcome this trend for three main reasons: (i) to obtain deeper insights into the generality of evolutionary models for SBD; (ii) to allow a priori testing of SBD predictions; and (iii) to avoid the confounding effects of phylogeny and social structure. Invertebrates and lower vertebrates should prove excellent models for experimental testing of evolutionary models without prior assumptions, particularly because social systems are highly diverse in such groups. However, mammals are highly diverse in terms of their social systems and patterns of SBD, and there is still much to be learned. Focus on exceptional model species (i.e. species displaying strong contrasts with related species and/or general trends) should prove particularly insightful. Studying the evolution of mammalian FBD in a comparative phylogenetic framework, for example, should provide a powerful means to explore the link between SBD and life history traits.

Acknowledgements

The authors would like to thank Laurent Lehmann and François Balloux for their helpful discussion on an earlier draft of this manuscript, and Louis Bernatchez, Linda Vigilant and an anonymous reviewer for invaluable comments and suggestions.

References

- Alberts SC, Altmann J (1995) Balancing costs and opportunities – dispersal in male baboons. *American Naturalist*, **145**, 279–306.
- Al-Zahery N, Semino O, Benuzzi G *et al.* (2003) Y-chromosome and mtDNA polymorphisms in Iraq, a crossroad of the early human dispersal and of post-Neolithic migrations. *Molecular Phylogenetics and Evolution*, **28**, 458–472.
- Austin JD, Davila JA, Loughheed SC, Boag PT (2003) Genetic evidence for female-biased dispersal in the bullfrog, *Rana catesbeiana* (Ranidae). *Molecular Ecology*, **12**, 3165–3172.
- Balloux F, Lugon-Moulin N (2002) The estimation of population differentiation with microsatellite markers. *Molecular Ecology*, **11**, 155–165.
- Banks SC, Skerratt LF, Taylor AC (2002) Female dispersal and relatedness structure in common wombats (*Vombatus ursinus*). *Journal of Zoology*, **256**, 389–399.
- Beaumont MA, Rannala B (2004) The Bayesian revolution in genetics. *Nature Reviews Genetics*, **5**, 251–261.
- Beaumont MA, Zhang WY, Balding DJ (2002) Approximate Bayesian computation in population genetics. *Genetics*, **162**, 2025–2035.
- Bekkevold D, Hansen MM, Mensberg KLD (2004) Genetic detection of sex-specific dispersal in historical and contemporary populations of anadromous brown trout *Salmo trutta*. *Molecular Ecology*, **13**, 1707–1712.
- Bengtsson BO (1978) Avoiding inbreeding – at what cost? *Journal of Theoretical Biology*, **73**, 439–444.
- Berry O, Tocher MD, Sarre SD (2004) Can assignment tests measure dispersal? *Molecular Ecology*, **13**, 551–561.
- Berteaux D, Boutin S (2000) Breeding dispersal in female North American red squirrels. *Ecology*, **81**, 1311–1326.
- Blundell GM, Ben-David M, Groves P, Bowyer RT, Geffen E (2002) Characteristics of sex-biased dispersal and gene flow in coastal river otters: implications for natural recolonization of extirpated populations. *Molecular Ecology*, **11**, 289–303.
- Bolnick DA, Bolnick DI, Smith DG (2006) Assymetric male and female genetic histories among native Americans from eastern North America. *Molecular Biology and Evolution*, **23**, 2161–2174.
- Bosch E, Calafell F, Rosser ZH *et al.* (2003) High level of male-biased Scandinavian admixture in Greenlandic Inuit shown by Y-chromosomal analysis. *Human Genetics*, **112**, 353–363.
- Bouteiller-Reuter C, Perrin N (2005) Sex-specific selective pressures on body mass in the greater white-toothed shrew, *Crocidura russula*. *Journal of Evolutionary Biology*, **18**, 290–300.
- Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biology Reviews*, **80**, 205–225.
- Bradbury JW, Vehrencamp SL (1976) Social organization and foraging in emballonurid bats. I: field studies. *Behavioral Ecology and Sociobiology*, **2**, 1–17.
- Bradbury JW, Vehrencamp SL (1977) Social-organization and foraging in emballonurid bats. III: mating systems. *Behavioral Ecology and Sociobiology*, **2**, 1–17.
- Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L (2004) Dispersed male networks in western gorillas. *Current Biology*, **14**, 510–513.
- Brockelman WY, Reichard U, Treesucon U, Raemaekers JJ (1998) Dispersal, pair formation and social structure in gibbons (*Hylobates lar*). *Behavioral Ecology and Sociobiology*, **42**, 329–339.
- Chesser RK, Baker RJ (1996) Effective sizes and dynamics of uniparentally and diparentally inherited genes. *Genetics*, **144**, 1225–1235.
- Clarke A (1978) Sex ratio and local resource competition in a prosimian primate. *Science*, **201**, 163–165.
- Clarke A, Saether B, Roskaft E (1997) Sex biases in avian dispersal: a reappraisal. *Oikos*, **79**, 429–438.
- Clobert J, Danchin E, Dhondt AA, Nichols JD (2001) *Dispersal*. Oxford University Press, Oxford.
- Clutton-Brock TH (1989) Female transfer and inbreeding avoidance in mammals. *Nature*, **337**, 70–71.
- Cockburn A, Scott MP, Scotts DJ (1985) Inbreeding avoidance and male-biased natal dispersal in *Antechinus* spp. (Marsupialia: Dasyuridae). *Animal Behaviour*, **33**, 908–915.
- Comins HN, Hamilton WD, May RM (1980) Evolutionary stable dispersal strategies. *Journal of Theoretical Biology*, **82**, 205–230.
- Cooke F, MacInnes CD, Prevett JP (1975) Gene flow between breeding populations of lesser snow goose. *Auk*, **92**, 493–510.
- Cornuet JM, Piry S, Luikart G, Estoup A, Solignac M (1999) New methods employing multilocus genotypes to select or exclude

- populations as origins of individuals. *Genetics*, **153**, 1989–2000.
- Crockett CM, Eisenberg JF (1987) Howlers: variations in group size and demography. In: *Primate Societies* (eds Smuts BB *et al.*), pp. 54–68. University of Chicago Press, Chicago.
- Dammhahn M, Kappeler PM (2005) Social system of *Microcebus berthae*, the world's smallest primate. *International Journal of Primatology*, **26**, 407–435.
- De Fraipont M, Clobert J, John H, Alder S (2000) Increased pre-natal maternal corticosterone promotes philopatry of offspring in common lizards *Lacerta vivipara*. *Journal of Animal Ecology*, **69**, 404–413.
- Destro-Bisol G, Donati F, Coia V *et al.* (2004) Variation of female and male lineages in sub-Saharan populations: the importance of sociocultural factors. *Molecular Biology and Evolution*, **21**, 1673–1682.
- Devillard S, Allaine D, Gaillard J-M, Pontier D (2004) Does social complexity lead to sex-biased dispersal in polygynous mammals? A test on ground-dwelling sciurids. *Behavioural Ecology*, **15**, 83–87.
- Dieckmann U, O'Hara B, Weisser W (1999) The evolutionary ecology of dispersal. *Trends in Ecology & Evolution*, **14**, 88–90.
- Dobson FS (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, **30**, 1183–1192.
- Eriksson J, Siedel H, Lukas D *et al.* (2006) Y-chromosome analysis confirms highly sex-biased dispersal and suggests a low male effective population size in bonobos (*Pan paniscus*). *Molecular Ecology*, **15**, 939–949.
- Erler A, Stoneking A, Kayser M (2004) Development of Y-chromosomal microsatellite markers for non-human primates. *Molecular Ecology*, **13**, 2921–2930.
- Favre L, Balloux F, Goudet J, Perrin N (1997) Female-biased dispersal in the monogamous mammal *Crocodylus russula*: evidence from field data and microsatellite patterns. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **264**, 127–132.
- Fedigan LM, Jack KM (2004) The demographic and reproductive context of male replacements in *Cebus capucinus*. *Behaviour*, **141**, 755–775.
- Fontanillas P, Petit E, Perrin N (2004) Estimating sex-specific dispersal rates with autosomal markers in hierarchically structured populations. *Evolution*, **58**, 886–894.
- Frame LH, Frame GW (1976) Female African wild dogs emigrate. *Nature*, **263**, 227–229.
- Fraser DJ, Lippe C, Bernatchez L (2004) Consequences of unequal population size, asymmetric gene flow and sex-biased dispersal on population structure in brook charr (*Salvelinus fontinalis*). *Molecular Ecology*, **13**, 67–80.
- Gandon S (1999) Kin competition, the cost of inbreeding and the evolution of dispersal. *Journal of Theoretical Biology*, **200**, 345–364.
- Goudet J, Perrin N, Waser P (2002) Tests for sex-biased dispersal using bi-parentally inherited genetic markers. *Molecular Ecology*, **11**, 1103–1114.
- Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, **28**, 1140–1162.
- Greenwood PJ, Harvey PH (1982) The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics*, **13**, 1–21.
- Guillaume F, Perrin N (2006) Joint evolution of dispersal and inbreeding load. *Genetics*, **173**, 479–509.
- Hamilton WD (1964) The genetical evolution of social behaviour I, II. *Journal of Theoretical Biology*, **7**, 1–52.
- Hamilton WD (1967) Extraordinary sex ratios. *Science*, **156**, 477–488.
- Hamilton G, Stoneking M, Excoffier L (2005a) Molecular analysis reveals tighter social regulation of immigration in patrilocal populations than in matrilocal populations. *Proceedings of the National Academy of Sciences, USA*, **102**, 7476–7480.
- Hamilton G, Currat M, Ray N *et al.* (2005b) Bayesian estimation of recent migration rates after a spatial expansion. *Genetics*, **170**, 409–417.
- Hamilton WD, May RM (1977) Dispersal in stable habitats. *Nature*, **269**, 578–581.
- Hammond RL, Lawson Handley LJ, Winney BJ, Bruford MW, Perrin N (2006) Genetic evidence for female-biased dispersal and gene flow in a polygynous primate. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **273**, 479–484.
- Hansson B, Bensch S, Hasselquist D (2003) A new approach to study dispersal: immigration of novel alleles reveals female-biased dispersal in great reed warblers. *Molecular Ecology*, **12**, 631–637.
- Harcourt AH, Stewart KJ, Fossey D (1976) Male emigration and female transfer in wild mountain gorillas. *Nature*, **263**, 226–227.
- Harris MA, Murie JO (1984) Inheritance of nest sites in female Columbian ground squirrels. *Behavioral Ecology and Sociobiology*, **15**, 97–102.
- Hellborg L, Ellegren H (2003) Y chromosome conserved anchor tagged sequences (YCATS) for the analysis of mammalian male-specific DNA. *Molecular Ecology*, **12**, 283–291.
- Hellborg L, Ellegren H (2004) Low levels of nucleotide diversity in mammalian Y chromosomes. *Molecular Biology and Evolution*, **21**, 158–163.
- Holekamp KE, Smale L (1995) Rapid change in offspring sex-ratios after clan fission in the spotted hyena. *American Naturalist*, **145**, 261–278.
- Hrdy SB (1977) *The Langurs of Abu*. Harvard University Press, Cambridge, Massachusetts.
- Hutchings JA, Gerber L (2002) Sex-biased dispersal in a salmonid fish. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, **269**, 2487–2493.
- Ishibashi Y, Saitoh T, Abe S, Yoshida MC (1997) Sex-related spatial kin structure in a spring population of grey-sided voles *Clethrionomys rufocanus* as revealed by mitochondrial and microsatellite DNA analyses. *Molecular Ecology*, **6**, 63–71.
- Izar P (2004) Female social relationships of *Cebus apella nigrilus* in a southeastern Atlantic forest: an analysis through ecological models of primate social evolution. *Behaviour*, **141**, 71–99.
- Jack KM, Fedigan L (2004a) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: patterns and causes of natal emigration. *Animal Behaviour*, **67**, 761–769.
- Jack KM, Fedigan L (2004b) Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: patterns and causes of secondary dispersal. *Animal Behaviour*, **67**, 771–782.
- Ji W, Sarre SD, Aitken N, Hankin RKS, Clout MN (2001) Sex-biased dispersal and a density-independent mating system in the Australian brushtail possum, as revealed by minisatellite DNA profiling. *Molecular Ecology*, **10**, 1527–1537.
- Johnson CN, Crossman DG (1991) Dispersal and social organization of the Northern hairy-nosed wombat *Lasiorhinus krefftii*. *Journal of Zoology*, **225**, 605–613.
- Johnson ML, Gaines MS (1990) Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annual Review of Ecology and Systematics*, **21**, 449–480.
- Kappeler PM, Wimmer B, Zinner D, Tautz D (2002) The hidden matrilineal structure of a solitary lemur: implications for primate

- social evolution. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **269**, 1755–1763.
- Kareem AM, Barnard CJ (1986) Kin recognition in mice — age, sex and parental effects. *Animal Behaviour*, **34**, 1814–1824.
- Kays RW, Gittleman JL, Wayne RK (2000) Microsatellite analysis of kinkajou social organization. *Molecular Ecology*, **9**, 743–751.
- Kerth G, Mayer F, Petit E (2002) Extreme sex-biased dispersal in the communally breeding, nonmigratory Bechstein's bat (*Myotis bechsteinii*). *Molecular Ecology*, **11**, 1491–1498.
- Knight ME, van Oppen MJH, Smith HL, Rico C, Hewitt GM, Turner GF (1999) Evidence for male-biased dispersal in Lake Malawi cichlids from microsatellites. *Molecular Ecology*, **8**, 1521–1527.
- Kumar V, Langstieh BT, Madhavi KV *et al.* (2006) Global patterns in human mitochondrial DNA and Y-chromosome variation caused by spatial instability of the local cultural processes. *PLoS Genetics*, **2**, 420–424.
- Kummer H (1968) *Social Organization of Hamadryas Baboons. A Field Study*. Chicago University Press, Chicago and London.
- Lambin X (1994) Sex-ratio variation in relation to female philopatry in Townsend voles. *Journal of Animal Ecology*, **63**, 945–953.
- Laporte V, Charlesworth B (2002) Effective population size and population subdivision in demographically structured populations. *Genetics*, **162**, 501–519.
- Lawler RR, Richard AF, Riley MA (2003) Genetic population structure of the white sifaka (*Propithecus verreauxi verreauxi*) at Beza Mahafaly Special Reserve, southwest Madagascar (1992–2001). *Molecular Ecology*, **12**, 2307–2317.
- Lawson Handley LJ, Perrin N (2006) Y chromosome microsatellite isolation from BAC clones in the greater white-toothed shrew (*Crocodyrus russula*). *Molecular Ecology Notes*, **6**, 276–279.
- Lawson Handley LJ, Hammond RL, Emaresi G, Reber A, Perrin N (2006a) Low Y chromosome variation in Saudi-Arabian hamadryas baboons (*Papio hamadryas hamadryas*). *Heredity*, **96**, 298–303.
- Lawson Handley LJ, Berset-Brändli L, Perrin N (2006b) Disentangling reasons for low Y chromosome variation in the greater-white toothed shrew (*Crocodyrus russula*). *Genetics*, **173**, 935–942.
- Le Galliard J-F, Gundersen G, Andreassen HP, Stenseth NC (2006) Natal dispersal, interactions among siblings and intra-sexual competition. *Behavioral Ecology*, **17**, 733–740.
- Lehmann L, Perrin N (2002) Altruism, dispersal, and phenotype-matching kin recognition. *American Naturalist*, **159**, 451–468.
- Lehmann L, Perrin N (2003) Inbreeding avoidance through kin recognition: Choosy females boost male dispersal. *American Naturalist*, **162**, 638–652.
- Malcolm JR, Marten K (1982) Natural selection and the communal rearing of pups in African wild dogs (*Lycaon pictus*). *Behavioral Ecology and Sociobiology*, **10**, 1–13.
- Manel S, Gaggiotti OE, Waples RS (2005) Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology & Evolution*, **20**, 136–142.
- Manning CJ, Wakeland EK, Potts WK (1992) Communal nesting patterns in mice implicate MHC genes in kin recognition. *Nature*, **360**, 581–583.
- Marsh CW (1979) Female transference and mate choice among Tana River red colobus. *Nature*, **281**, 568–569.
- McFarland Symington M (1987) Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behavioural Ecology and Sociobiology*, **20**, 421–425.
- McNutt JW (1996) Sex-biased dispersal in African wild dogs, *Lycaon pictus*. *Animal Behaviour*, **52**, 1067–1077.
- Melnick DJ, Pearl MC (1987) Cercopithecines in multimale groups: genetic diversity and population structure. In: *Primate Societies* (eds Smuts BB *et al.*), pp. 121–134. University of Chicago Press, Chicago.
- Mesa NR, Mondragon MC, Soto ID *et al.* (2000) Autosomal, mtDNA, and Y-chromosome diversity in Amerinds: pre- and post-Columbian patterns of gene flow in South America. *American Journal of Human Genetics*, **67**, 1277–1286.
- Monard AM, Duncan P (1996) Consequences of natal dispersal in female horses. *Animal Behaviour*, **52**, 565–579.
- Moore J, Ali R (1984) Are dispersal and inbreeding avoidance related? *Animal Behaviour*, **32**, 94–112.
- Mossman CA, Waser PM (1999) Genetic detection of sex-biased dispersal. *Molecular Ecology*, **8**, 1063–1067.
- Motro U (1991) Avoiding inbreeding and sibling competition: the evolution of sexual dimorphism for dispersal. *American Naturalist*, **137**, 108–115.
- Möller LM, Beheregaray LB (2004) Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Molecular Ecology*, **13**, 1607–1612.
- Murrell DJ, Travis MJ, Dytham C (2002) The evolution of dispersal distance in spatially-structured populations. *Oikos*, **97**, 229–236.
- Mutschler T, Nievergelt CM, Feistner ATC (2000) Social organization of the Alaotran gentle lemur (*Haplorhina griseus alaotrensis*). *American Journal of Primatology*, **50**, 9–24.
- Nakagawa S, Waas JR (2004) 'O sibling, where art thou?' — a review of avian sibling recognition with respect to the mammalian literature. *Biological Reviews*, **79**, 101–119.
- Natoli A, Birkun A, Aguilar A, Lopez A, Hoelzel AR (2005) Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **272**, 1217–1226.
- Nishida T, Hasegawa M (1987) Chimpanzees and bonobos: Cooperative relationships among males. In: *Primate Societies* (eds Smuts BB *et al.*), pp. 165–177. University of Chicago Press, Chicago.
- Nishimura A (2003) Reproductive parameters of wild female *Lagothrix lagotricha*. *International Journal of Primatology*, **24**, 707–722.
- Nunes S, Zugger PA, Engh AL, Reinhart KO, Holekamp KE (1997) Why do female Belding's ground squirrels disperse away from food resources? *Behavioral Ecology and Sociobiology*, **40**, 199–207.
- Olupot W, Waser PM (2001) Correlates of intergroup transfer in male grey-cheeked mangabeys. *International Journal of Primatology*, **22**, 169–187.
- Oota H, Settheethamishida W, Tiwawech D, Ishida T, Stoneking M (2001) Human mtDNA and Y-chromosomal variation is correlated with matrilineal versus patrilineal residence. *Nature*, **29**, 20–21.
- Packer C (1979) Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Animal Behaviour*, **27**, 1–36.
- Packer C, Pusey AE (1987) Intrasexual cooperation and the sex-ratio in African lions. *American Naturalist*, **130**, 636–642.
- Paetkau D, Calvert W, Stirling I, Strobeck C (1995) Microsatellite analysis of population structure in Canadian polar bears. *Molecular Ecology*, **4**, 347–354.
- Palo JU, Lesbarreres D, Schmeller DS, Primmer CR, Merila J (2004) Microsatellite marker data suggest sex-biased dispersal in the common frog *Rana temporaria*. *Molecular Ecology*, **13**, 2865–2869.
- Pardini AT, Jones CS, Noble LR *et al.* (2001) Sex-biased dispersal of great white sharks. *Nature*, **412**, 139–140.
- Parr LA, de Waal FBM (1999) Visual kin recognition in chimpanzees. *Nature*, **399**, 647–648.

- Peakall R, Ruibal M, Lindenmayer DB (2003) Spatial autocorrelation analysis offers new insights into gene flow in the Australian bush rat, *Rattus fuscipes*. *Evolution*, **57**, 1182–1195.
- Pereira ME, Weiss ML (1991) Female mate choice, male migration, and the threat of infanticide in ringtailed lemurs. *Behavioral Ecology and Sociobiology*, **28**, 141–152.
- Perez-Lezaun A, Calafell F, Comas D *et al.* (1999) Sex-specific migration patterns in central Asian populations, revealed by analysis of Y-chromosome short tandem repeats and mtDNA. *American Journal of Human Genetics*, **65**, 208–219.
- Perrin N, Goudet J (2001) Inbreeding, kinship and the evolution of natal dispersal. In: *Dispersal* (eds Clobert J *et al.*), pp. 123–142. Oxford University Press, Oxford.
- Perrin N, Lehmann L (2001) Is sociality driven by the costs of dispersal or the benefits of philopatry? A role for kin-discrimination mechanisms. *American Naturalist*, **158**, 471–483.
- Perrin N, Mazalov V (1999) Dispersal and inbreeding avoidance. *American Naturalist*, **154**, 282–292.
- Perrin N, Mazalov V (2000) Local competition, inbreeding and the evolution of sex-biased dispersal. *American Naturalist*, **155**, 116–127.
- Petit E, Balloux F, Goudet J (2001) Sex-biased dispersal in a migratory bat: a characterization using sex-specific demographic parameters. *Evolution*, **55**, 635–640.
- Piertney SB, MacColl ADC, Bacon PJ, Dallas JF (1998) Local genetic structure in red grouse (*Lagopus lagopus scoticus*): evidence from microsatellite DNA markers. *Molecular Ecology*, **7**, 1645–1654.
- Pope TR (2000) Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). *Behavioral Ecology and Sociobiology*, **48**, 253–267.
- Price K, Boutin S (1993) Territorial bequeathal by red squirrel mothers. *Behavioural Ecology*, **4**, 144–150.
- Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.
- Prugnolle F, de Meeüs T (2002) Inferring sex-biased dispersal from population genetic tools: a review. *Heredity*, **88**, 161–165.
- Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution*, **2**, 295–299.
- Pusey AE, Packer C (1987) Dispersal and philopatry. In: *Primate Societies* (eds Smuts BB *et al.*), pp. 250–266. University of Chicago Press, Chicago, Illinois.
- Radespiel L, Lutermaier H, Schmelting B, Bruford MW, Zimmermann E (2003) Patterns and dynamics of sex-biased dispersal in a nocturnal primate, the grey mouse lemur, *Microcebus murinus*. *Animal Behaviour*, **65**, 709–719.
- Radespiel U, Sarikaya Z, Zimmermann E, Bruford MW (2001) Sociogenetic structure in a free-living nocturnal primate population: sex-specific differences in the grey mouse lemur (*Microcebus murinus*). *Behavioral Ecology and Sociobiology*, **50**, 493–502.
- Rannala B, Mountain JL (1997) Detecting immigration by using multilocus genotypes. *Proceedings of the National Academy of Sciences, USA*, **94**, 9197–9201.
- Ribble DO (1992) Dispersal in a monogamous rodent, *Peromyscus californicus*. *Ecology*, **73**, 859–866.
- Richard AF, Rakotomanga P, Schwartz M (1993) Dispersal by *Propithecus verreauxi* at Beza-Mahafaly, Madagascar — 1984–91. *American Journal of Primatology*, **30**, 1–20.
- Robinson JG, Janson CH (1987) Capuchins, squirrel monkeys and Atelines: socio-ecological convergence with Old World primates. In: *Primate Societies* (eds Smuts BB *et al.*), pp. 69–82. University of Chicago Press, Chicago, Illinois.
- Ronce O, Olivieri I, Clobert J, Danchin E (2001) Perspectives on the study of dispersal evolution. In: *Dispersal* (ed. Clobert J), pp. 314–357. Oxford University Press, Oxford.
- Rousset F, Gandon S (2002) Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *Journal of Evolutionary Biology*, **15**, 515–523.
- Sarno RJ, Bank MS, Stern HS, Franklin WL (2003) Forced dispersal of juvenile guanacos (*Lama guanicoe*): causes, variation, and fates of individuals dispersing at different times. *Behavioral Ecology and Sociobiology*, **54**, 22–29.
- Schülke O (2003) To breed or not to breed — food competition and other factors involved in female breeding decisions in the pair-living nocturnal fork-marked lemur (*Phaner furcifer*). *Behavioral Ecology and Sociobiology*, **55**, 11–21.
- Scribner KT, Peterson MR, Fields RL, Talbot SL, Pearce JM, Chesser RK (2001) Sex-biased gene flow in spectacled eiders (Anatidae): inferences from molecular markers with contrasting modes of inheritance. *Evolution*, **55**, 2105–2115.
- Seielstad M (2000) Asymmetries in the maternal and paternal genetic histories of Colombian populations. *American Journal of Human Genetics*, **67**, 1062–1066.
- Seielstad MT, Minch E, Cavalli-Sforza LL (1998) Genetic evidence for a higher female migration rate in humans. *Nature Genetics*, **20**, 278–280.
- Skerratt LF, Skerratt JHL, Banks S, Martin R, Handasyde K (2004) Aspects of the ecology of common wombats (*Vombatus ursinus*) at high density on pastoral land in Victoria. *Australian Journal of Zoology*, **52**, 303–330.
- Smale L, Nunes S, Holekamp KE (1997) Sexually dimorphic dispersal in mammals: patterns, causes and consequences. *Advances in the Study of Behavior*, **26**, 181–250.
- Stammach E (1987) Desert, forest and montane baboons: multilevel societies. In: *Primate Societies* (eds Smuts BB *et al.*), pp. 112–120. University of Chicago Press, Chicago and London.
- Sterck E (1997) Determinants of female dispersal in Thomas's langurs. *American Journal of Primatology*, **43**, 179–198.
- Sterck E (1998) Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance? *American Journal of Primatology*, **44**, 235–254.
- Stewart KJ, Harcourt AH (1987) Gorillas: variation in female relationships. In: *Primate Societies* (eds Smuts BB *et al.*), pp. 155–164. University of Chicago Press, Chicago.
- Stokes EJ, Parnell RJ, Olejniczak C (2003) Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). *Behavioral Ecology and Sociobiology*, **54**, 329–339.
- Strier KB, Ziegler TE (2000) Lack of pubertal influences on female dispersal in muriqui monkeys, *Brachyteles arachnoides*. *Animal Behaviour*, **59**, 849–860.
- Struhsaker TT, Leland L (1987) Colobines: infanticide by adult males. In: *Primate Societies* (eds Smuts BB *et al.*), pp. 83–97. University of Chicago Press, Chicago.
- Surridge AK, Ibrahim KM, Bell DJ *et al.* (1999) Fine-scale genetic structuring in a natural population of European wild rabbits (*Oryctolagus cuniculus*). *Molecular Ecology*, **8**, 299–307.
- Sussman RW (1992) Male life history and intergroup mobility among ringtailed lemurs (*Lemur catta*). *International Journal of Primatology*, **13**, 395–413.
- Sweitzer RA, Berger J (1998) Evidence for female-biased dispersal in North American porcupines (*Erethizon dorsatum*). *Journal of Zoology*, **244**, 159–166.
- Taylor MI, Morley JL, Rico C, Balshine S (2003) Evidence for genetic monogamy and female-biased dispersal in the biparental

- mouthbrooding cichlid *Eretmodus cyanostictus* from Lake Tanganyika. *Molecular Ecology*, **12**, 3173–3177.
- Travis JMJ, French DR (2000) Dispersal functions and spatial models: expanding our dispersal toolbox. *Ecology Letters*, **3**, 163–165.
- Vitalis R (2002) Sex-specific genetic differentiation and coalescence times: estimating sex-biased dispersal rates. *Molecular Ecology*, **11**, 125–138.
- Waser PM (1985) Does competition drive dispersal? *Ecology*, **66**, 1170–1175.
- Waser PM, Austad SN, Keane B (1986) When should animals tolerate inbreeding? *American Naturalist*, **128**, 529–537.
- Waser PM, Creel SR, Lucas JR (1994) Death and disappearance — estimating mortality risks associated with philopatry and dispersal. *Behavioral Ecology*, **5**, 135–141.
- Waser PM, Strobeck C (1998) Genetic signatures of interpopulation dispersal. *Trends in Ecology & Evolution*, **13**, 43–44.
- Watson A, Moss R, Parr R, Mountford MD, Rothery P (1994) Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. *Journal of Animal Ecology*, **63**, 39–50.
- Weir BS, Cockerham CC (1984) Estimating F statistics for the analysis of population structure. *Evolution*, **38**, 1358–1370.
- Whitlock MC, McCauley DE (1999) Indirect measures of gene flow and migration: F_{ST} does not equal $1/(4Nm+1)$. *Heredity*, **82**, 117–125.
- Wilder JA, Kingan SB, Mobasher Z, Pilkington MM, Hammer MF (2004) Global patterns of human mitochondrial DNA and Y-chromosome structure are not influenced by higher migration rates of females versus males. *Nature Genetics*, **36**, 1122–1125.
- Wilkins JF, Marlowe FW (2006) Sex-biased migration in humans: what should we expect from genetic data? *Bioessays*, **28**, 290–300.
- Wimmer B, Kappeler PM (2002) The effects of sexual selection and life history on the genetic structure of red-fronted lemur, *Eulemur fulvus rufus*, groups. *Animal Behaviour*, **64**, 557–568.
- Winters JB, Waser PM (2003) Gene dispersal and outbreeding in a philopatric mammal. *Molecular Ecology*, **12**, 2251–2259.
- Wolff JO (1992) Parents suppress reproduction and stimulate dispersal in opposite-sex juvenile white-footed mice. *Nature*, **359**, 409–410.
- Wolff JO (1994) More on juvenile dispersal in mammals. *Oikos*, **71**, 349–352.
- Wood ET, Stover DA, Ehret C *et al.* (2005) Contrasting patterns of Y chromosome and mtDNA variation in Africa: evidence for sex-biased demographic processes. *European Journal of Human Genetics*, **13**, 867–876.
- Wright S (1931) Evolution in Mendelian populations. *Genetics*, **16**, 97–159.
- Wright S (1943) Isolation by distance. *Genetics*, **28**, 114–138.
- Wright TF, Rodriguez AM, Fleischer RC (2005) Vocal dialects, sex-biased dispersal, and microsatellite population structure in the parrot *Amazona auropalliata*. *Molecular Ecology*, **14**, 1197–1205.

Lori Handley's main research interests are in empirical evolutionary genetics of animal populations, for example the inference of demographic processes and their consequences for the genetic make up of populations. Nicolas Perrin is investigating the ecology and evolution of dispersal along empirical and theoretical lines, including game-theoretical modelling, computer simulations, and the testing of demographic inferences from genetic data.
