

The dynamics of operational sex ratios and competition for mates

Charlotta Kvarnemo and Ingrid Ahnesjö

Questions such as when should females compete for access to males, and how intense contest competition for mating partners should be, are central to behavioural ecology and to the study of sexual selection. To answer them, the concept of operational sex ratio (OSR – the ratio of males to females ready to mate; Box 1) is a central tool that in recent years has become more prominent in empirical studies and that has also received considerable theoretical attention¹⁻³. The concept is important since OSR is a main determinant of the opportunity for sexual selection^{2,4,5}, and it subsumes a number of important factors into one term (Box 1 and Fig. 1). A bias in OSR can predict which sex will compete for access to mates and how intense this competition will be (Fig. 2): as the OSR deviates from equality, more-intense mating competition is predicted, and the sex that is in excess, which is predicted to become the predominant competitor for access to mating partners, will be under stronger sexual selection. The term 'mating competition' is used here not only to describe violent acts between competitors, but also more-subtle expressions in displays and courtship resulting in dominance hierarchies and reproductive inhibition.

OSR has successfully been used to explain cases where males and females under different circumstances alternate as the predominant competitor for mates, for example, in some species of bush crickets⁶⁻¹⁰. It is, however, important to recognize that although both sexes simultaneously may be competing for mates, the bias in OSR predicts which sex is the predominant competitor (Fig. 2). Furthermore, OSR is a good predictor of contest competition for mates and to some extent mate choice, but will not in general predict

In sexually reproducing animals, individuals of one sex may have to compete for access to mating partners of the opposite sex. The operational sex ratio (OSR) is central in predicting the intensity of mating competition and which sex is competing for which. Thanks to recent theoretical and empirical advances, particularly by exploring the concept of OSR, sexual selection studies today are becoming more fine-tuned and dynamic. The original role of parental investment in predicting sexual selection has recently been complemented by the use of sexual differences in potential reproductive rates (PRR).

Charlotta Kvarnemo is at the Dept of Zoology, University of Western Australia, Nedlands, WA 6009, Australia; Ingrid Ahnesjö is at the Dept of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden (Ingrid.Ahnesjo@zoologi.uu.se).

the prevalence or intensity of other mechanisms of sexual selection (*sensu* Ref. 11), such as sperm competition, infanticide or coercion.

OSR, in turn, is influenced by the sexual difference in potential reproductive rate (PRR; see Box 2 and Fig. 1), such that there are more individuals ready to mate, at any one time, of the sex with the potential to reproduce at a higher rate². This has been demonstrated, for instance, in giant water bugs¹², pipefishes¹³⁻¹⁵ and the sand goby^{16,17}.

Traditionally, sexual selection has been assumed to be governed by the sexes' relative parental investment, which is 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring'¹⁸. In theory, the sex with the lower parental investment will be the sex towards which OSR is biased. However, parental investment is empirically inaccessible, as it has proven extremely difficult to measure the cost in terms of future offspring. Consequently, parental expenditure (or parental input), measured as resources spent on the production of offspring regardless of the fitness costs^{19,20}, has often been used to approximate parental investment². Moreover, the two sexes may make the expenditure in different currencies, time or energy, making sexual comparisons difficult²¹. However, a difference between the sexes in parental investment should lead to a difference in the frequency with which males and females can engage in reproductive events. Therefore, as has recently been suggested²², relative parental investment may be measured as relative PRR, since the cost of reproduction can be viewed as the parent's 'time out' (Box 1), a principal component of PRR (Box 2), which in turn relates directly to the OSR.

Box 1. The operational sex ratio (OSR)

Definition: The OSR is the ratio of males and females who are ready to mate in a population at a given time⁴. Alternatively, the reproductive cycle of an individual is divided between being ready to mate ('time in') and not being ready to mate ('time out')². The OSR is then the time fraction of a reproductive cycle when an average male is ready to mate, divided by the time fraction an average female is ready to mate, times the adult sex ratio. In sexually reproducing animals, the realized reproductive rates of the sexes are equal, on average. In contrast, 'time out' (e.g. time devoted to parental care or egg production), often differs between the sexes, and the shorter 'time out' of a sex, the higher potential reproductive rate (PRR; Box 2). If the adult sex ratio is even, then the sexual difference in PRR will be a main determinant of OSR and direction and intensity of mating competition.

Empirical measure: OSR can be measured either as (1) the number of males and females prepared to mate, or (2) the mean 'time in' of each sex, in a population over a relevant time. To create a finite scale, OSR is preferably calculated as a percentage, that is the number, or 'time in', of:

$$\text{males prepared to mate} / (\text{males} + \text{females prepared to mate})$$

OSR will then range from 0%, when only females are prepared to mate, to 100%, when only males are ready to mate (cf. Refs 14,28).

Shifts in OSR and in sex roles

Though typical sex roles can be attributed to most animals, recent studies have produced abundant examples of species showing predominant male competition for mates in some populations but reversed sex roles (that is female competition) in others, or even switching of sex roles within a population over time. In some

species of bush crickets, in which the males produce energetically expensive spermatophores, which represent a nutritive donation to the female, males compete for matings when high-quality food is abundant, since males can then produce spermatophores more rapidly than females produce eggs. Consequently, more males than females are ready to mate – the OSR is male-biased. In contrast, when food is scarce, males take longer to produce spermatophores and the OSR is female-biased, a situation that is reinforced by females ‘foraging for spermatophores’ by repeated matings, and as a result females become the more competitive sex^{6–10}. Similarly, in the blennid fish *Salaria pavo*, where males provide parental care in nests, males court females in most populations. However, the reverse is true in a population with a severe nest-site shortage, where the OSR is biased towards females because only a small proportion of the males acquire nests but all females are producing eggs²³. In all these studies, varying environmental factors, including monopolizable resources required for being prepared to mate, change the OSR in a dynamic fashion, leading to shifts in sex roles (*sensu* Ref. 24) and sexual selection.

OSR and intensity in competition for mates

Changes in OSR can alter the intensity of competition for mates (Fig. 2), without necessarily shifting sex roles. In many cases, such variation in OSR will occur within populations, usually over the course of a breeding season. For instance, in a population of the sex-role-reversed pipefish (*Syngnathus typhle*) OSR varied over the season, becoming more female-biased as males became pregnant and so unavailable for matings¹⁴. As predicted, the proportion of female–female encounters, indicating competition among females, increased with the degree of female bias in OSR¹⁴. In a sex-role-reversed shorebird, Wilson’s phalarope (*Phalaropus tricolor*), the intensity of female–female competition became weaker as OSR became more male-biased as more males arrived on the breeding grounds²⁵. Such a pattern has also been documented in the Japanese medaka fish, *Oryzias latipes*, where OSR, experimentally manipulated in terms of degree of female synchrony, influenced the intensity of male–male competition²⁶.

Both OSR and intensity of mating competition commonly vary among populations, a finding that has been corroborated experimentally. For example, in the marine isopod *Idotea baltica*, males prolonged the duration of precopulatory guarding (that is, males started to guard earlier) as a result of increased male–male competition in groups with male-biased OSRs²⁷. Similarly, in the common spider mite (*Tetranychus urticae*) male–male competition increased as predicted under increasingly male-biased OSR, and larger male size was favoured accordingly²⁸. Finally, in the sand goby (*Pomatoschistus minutus*), not only were males found to compete more frequently under male bias than under female bias, but also females were found to increase their competitive interactions under female bias, even though males were the predominant competitors²⁹.

Factors affecting OSR

Factors other than PRR (see below) that may affect OSR include biased adult sex ratios, differences between the sexes in age at maturity, reproductive longevity, migration schedules, spatial distribution, and mortality during the reproductive season (reviewed in Ref. 1). The cactophilic fruitfly (*Drosophila pachea*) provides a fascinating example of how a sexual difference in age at maturity can affect OSR: males, which produce giant sperm, need four times as many

days as females to reach sexual maturity and consequently OSR is female-biased most of the time³⁰. Migration schedules in several birds differ between the sexes, creating seasonal changes in OSR²⁵. Water striders often demonstrate variation between the sexes in spatial distributions and thus OSRs^{31,32}. Furthermore, predation on broods (including filial cannibalism) may make a parent ready to mate again, which will influence the bias in OSR³³.

As any sexual difference in PRR will greatly influence a population’s OSR^{7,14,17,34} (Boxes 1 and 2), factors that affect the PRR become of special interest. These include, for instance, physiological constraints and sensitivity to environmental factors, like food, temperature and nest site availability. Many of these environmental factors will affect the OSR dynamically as illustrated by the following examples.

Temperature typically varies in most temperate regions, and this can affect the intensity of sexual selection in many ectotherms. In some species of giant water bugs, water temperature, and thus season, has been shown to considerably affect the sexual difference in PRR and OSR, because temperature influences male brooding time, egg synthesizing time and clutch size in females¹². Furthermore, in the facultatively sex-role-reversed Majorcan midwife toad (*Alytes muletensis*) (S. Bush, PhD thesis, University of East Anglia, UK, 1993), the sex-role-reversed pipefish¹⁵ and the sand goby (which has conventional sex roles)¹⁶, increased ambient temperature has been shown to affect the sexual difference in PRR by increasing the reproductive rates of males (Fig. 3). As temperature changes, the sexual difference in PRR, and

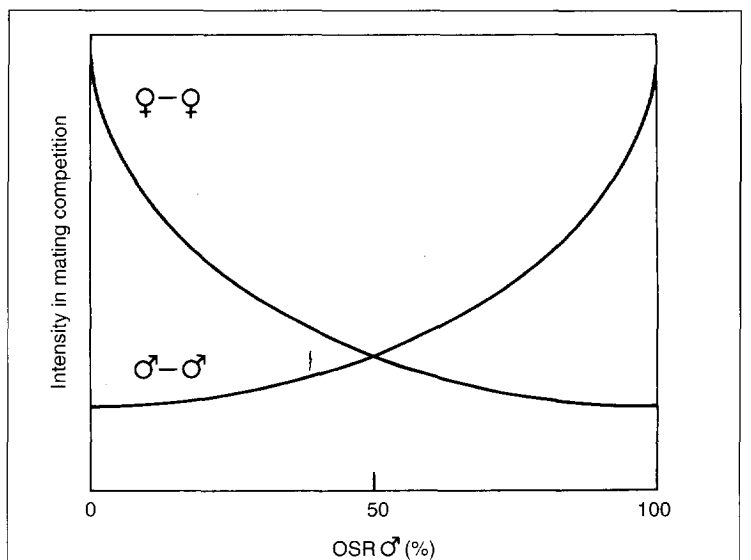
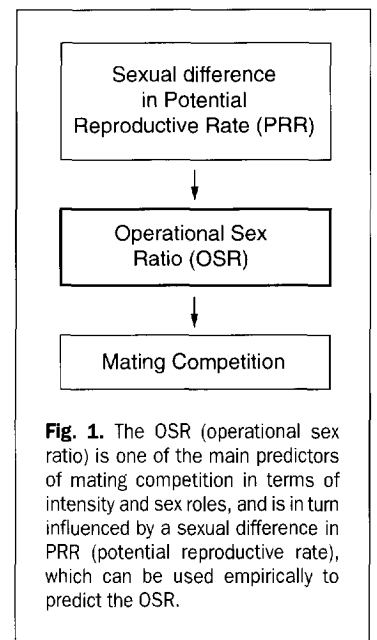


Fig. 2. The intensity of competition for access to mates will become more intense as the OSR (operational sex ratio) deviates from 50%, in either direction. Any excess of either sex will be least when the OSR is around 50%. When the OSR exceeds 50%, more males than females will be ready to mate in the population and males are predicted to be the predominant competitors, whereas at an OSR below 50%, females would become the predominant competitors. The exact shape and position of these curves probably vary between cases.

Box 2. The potential reproductive rate (PRR)

Definition: The PRR is either defined as 'the maximum number of independent offspring that parents can produce per unit time'¹, or, mathematically as the inversed 'time out' for males and females, respectively². PRR for each sex, when not constrained by availability of mating partners, deals with the population's mean value of individual maximum reproductive rates, which has been unclear in these definitions. The sexual difference in PRR, in the population, is then influencing the OSR.

Empirical measure: PRR is measured either as number of offspring produced per unit time or as the 'time out', for males and females, respectively, when mating partners are freely available but all other constraints in terms of environmental factors (such as food, number and sizes of nest sites, temperature) remain. Thus, the sexual difference in PRR has to be estimated experimentally for a sample of the population, and the sexual difference in PRR will in turn predict the OSR¹³⁻¹⁶.

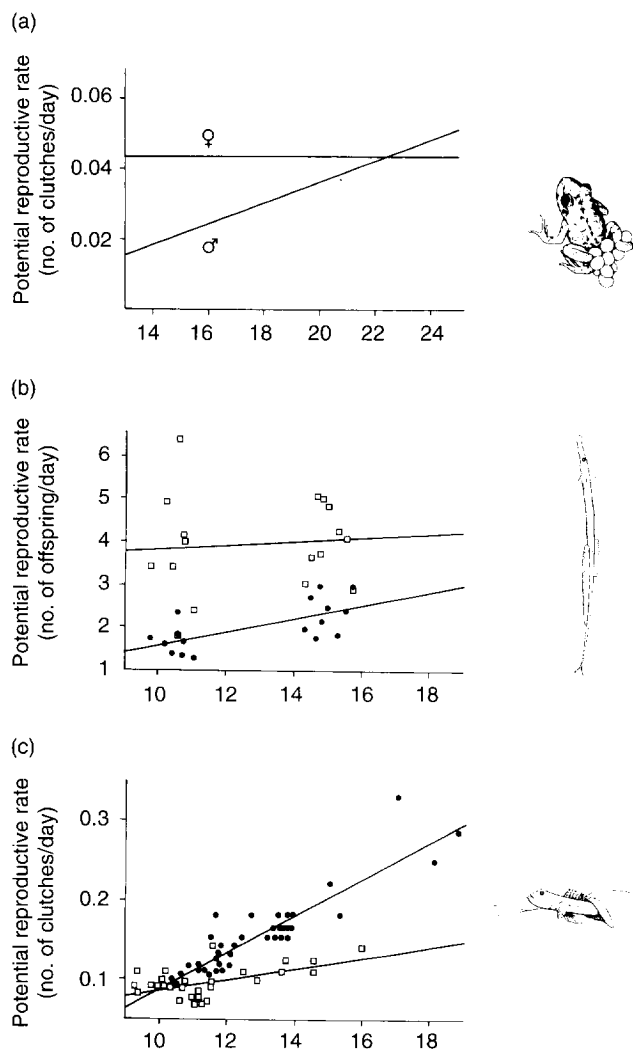


Fig. 3. Variation in ambient temperature may considerably affect both the sexual difference in potential reproductive rates (PRR) and the operational sex ratio (OSR). This is found in three species with paternal care: (a) the sex-role-reversed Majorcan midwife toad (*Alytes muletensis*) (S. Bush, PhD thesis, University of East Anglia, UK, 1993); (b) the sex-role-reversed pipefish (*Syngnathus typhle*)¹⁵; (c) the sand goby (*Pomatoschistus minutus*) with conventional sex roles¹⁶. Filled circles, males; unfilled squares, females. Characteristically, increased temperature increased the PRR of males more than of females. OSR is biased towards the sex with the higher PRR, which, therefore, is predicted to compete more intensely for matings than the other sex, and even more so when the discrepancy in PRR is larger. Congruently, male sand gobies are found to compete more intensely in warmer water¹⁷, and pipefish females compete more intensely in colder water¹⁴. Data in (a) are published with kind permission of S. Bush; data in (b) and (c) are derived from Refs 15 and 16, with permission. Drawings are by (a) L. Wedin, after photograph by S. Bush, (b) A. Ulfstrand, and (c) L. Wedin.

consequently OSR and levels of sexual selection, change over the breeding season in these species.

When nest site availability differs between populations, it may also affect the sexual difference in PRR and OSR, since the PRR of the nest-holding sex may be reduced considerably by scarcity of nest sites, as in the blennid fish²³. In a sand goby population with a pronounced nest-site shortage, male mating success was primarily determined by intrasexual competition over nest sites and only marginally by female choice. In a population with nest sites in excess, however, any male could get hold of a nest site, and consequently, mating success to a larger extent was determined by female mate choice³⁵.

Obviously, any sexual difference in PRR is likely to be influenced simultaneously by several factors of varying impact. The PRR is, furthermore, often positively related to body size and/or age, and differently so in the sexes¹⁵, and thus the OSR, as a consequence of a sexual difference in PRR, will be sensitive to the size- and age-distributions in a population.

Future directions

The usefulness of the concept of OSR derives from its dynamic relationship with various environmental factors, which may vary over time and in space. Future empirical and theoretical work, however, will have to address the following questions: (1) how to unify the verbal and mathematical definitions of OSR and PRR (Boxes 1 and 2); (2) how to count OSR empirically; (3) how does variance in mate quality affect mating competition; and (4) how does mate choice relate to OSR? However, none of the problems involved in these questions should devalue the heuristic value of OSR as a concept⁴.

(1) At present, OSR can be measured as frequencies of individuals ready to mate, and PRR can be measured as number of offspring produced per unit time, or both OSR and PRR can be calculated from 'time in' versus 'time out' of the sexes (Boxes 1 and 2). These definitions of PRR and OSR are, unfortunately, not always congruent: for instance, an individual which interrupts its 'time out' will be prepared to remate sooner, regardless of how many independent offspring it produced. Furthermore, when one sex is able to raise multiple clutches (from the other sex) simultaneously, this will not be reflected when measuring their 'time out', unless divided by number of offspring, or number of clutches that are brooded simultaneously^{12,13,16}. Recent elaborations have, however, included situations where a single reproductive event involves 'the times out' of more than one individual of each sex²².

(2) When measuring OSR, it is important to define carefully the specific time span and population in focus, and also whether or not an individual is ready to mate. In some animals, the major changes in OSR occur at an annual level, as in the adder (*Vipera berus*), where OSR is determined mainly by the adult sex ratio³⁶: competition between males was found to be stronger in years when the sex ratio was more male-biased. In other animals, the total adult sex ratio is of minor importance, while momentary differences in the distribution of the sexes are central, as in lekking ruff, *Philomachus pugnax*³⁷. When estimating OSR in a population by direct counts, it is usually hard to assess whether or not an individual is prepared to mate. If the non-mating status (for example brooding individuals) is easier to determine, an alternative approach is suggested in the model by Clutton-Brock and Parker² (Box 1): to calculate the adult sex ratio and then exclude all individuals who are *not* ready to mate (e.g. Ref. 14), or to calculate the average time fraction of the

reproductive cycle when each sex is *not* ready to mate. When a certain resource, like nest sites or food, is required for mating, the competition over that resource will not be predicted by OSR, as OSR only predicts the actual competition for mating partners. Taking the sand goby as an example, a male is not prepared to mate until he has acquired a nest site, nor is a male guarding a nest full of eggs ready to mate until the eggs have hatched, and nor can a recently spawned female respawn until new eggs have matured¹⁶. Similarly, in the pipefish, where males care for eggs in a brood pouch, once the pouch is filled the male is not available for further matings until after parturition, whereas females continuously produce eggs^{13,14}.

(3) An important and exciting task is to continue to examine competition for mates when individuals vary substantially in quality. Then, only a subset of members of the opposite sex are competed for as mates^{38,39}, and the OSR is no longer a sufficient predictor of mating competition^{2,3,40}.

(4) OSR and degree of choosiness are related, as the sex in shortage may afford to be selective (without losing mating opportunities) and may have many potential mates to choose among. In accordance, the sex in shortage has been demonstrated to be the more choosy sex, for example, in pipefish⁴¹ and field crickets⁴². This, of course, does not preclude the predominantly competitive sex from being selective as well^{34,41,43}, or the other sex to be unselective and still mate with fitter mates as an outcome of contest competition⁴⁴. However, other recent studies have shown that in some species the competing sex may, in fact, also be the most choosy sex^{38,39}. A large variation in mate quality may actually promote both a high selectivity and intense competition over those high-quality mates³⁸. Furthermore, an individual of good quality may have better prospects of being selective in its mate choice than an individual of poorer quality, resulting in assortative matings⁴⁰. Recently it has been pointed out that the costs of being choosy, rather than the benefits, should decide which sex will actually be the more selective^{5,11,45}. Finally, further factors such as mate density, predation risk and time of the season may also affect the costs and benefits of mate choice⁴⁶. Thus, the relationship between OSR and choosiness is more complex than that between OSR and mating competition, and we view this as an area that certainly needs more empirical, as well as theoretical, attention.

Conclusion

We encourage an increased use of OSR, which will help us to achieve a higher resolution, within and between populations, of changes in mating competition with all the consequent effects for the operation of sexual selection. Estimating the sexual differences in PRR, with due consideration to all the factors influencing it, has turned out to be an especially fruitful approach to predicting and understanding the dynamic in the OSR. The effects of variance in mate quality on mating competition, mate choice and the OSR are exciting fields for future empirical and theoretical development.

Acknowledgements

We are most grateful to Anders Berglund, Elisabet Forsgren, Leigh Simmons, Staffan Ulfstrand and referees for comments on the manuscript, to Sarah Bush for providing Fig. 3a, and to Lars Wedin and Astrid Ulfstrand for drawing the figures.

References

- Clutton-Brock, T.H. and Vincent, A.C.J. (1991) **Sexual selection and the potential reproductive rate of males and females**, *Nature* 351, 58–60
- Clutton-Brock, T.H. and Parker, G.A. (1992) **Potential reproductive rates and the operation of sexual selection**, *Q. Rev. Biol.* 67, 437–456
- Owens, I.P.F. and Thompson, D.B.A. (1994) **Sex differences, sex ratios and sex roles**, *Proc. R. Soc. London Ser. B* 258, 93–99
- Emlen, S.T. and Oring, L.W. (1977) **Ecology, sexual selection, and the evolution of mating systems**, *Science* 197, 215–223
- Reynolds, J.D. (1996) **Animal breeding systems**, *Trends Ecol. Evol.* 11, 68–72
- Gwynne, D.T. and Simmons, L.W. (1990) **Experimental reversal of courtship roles in an insect**, *Nature* 346, 172–174
- Gwynne, D.T. (1990) **Testing parental investment and the control of sexual selection in katydids: the operational sex ratio**, *Am. Nat.* 136, 474–484
- Simmons, L.W. and Bailey, W.J. (1990) **Resource influenced sex roles of zaprochiline tettigoniids (Orthoptera: Tettigoniidae)**, *Evolution* 44, 1853–1868
- Simmons, L.W. (1992) **Quantification of role reversal in relative parental investment in a bushcricket**, *Nature* 358, 61–63
- Simmons, L.W. (1995) **Relative parental expenditure, potential reproductive rates, and the control of sexual selection in katydids**, *Am. Nat.* 145, 797–808
- Andersson, M. and Iwasa, Y. (1996) **Sexual selection**, *Trends Ecol. Evol.* 11, 53–58
- Kruse, K.C. (1990) **Male backspace availability in the giant waterbug (*Belostoma flumineum* Say)**, *Behav. Ecol. Sociobiol.* 26, 281–289
- Berglund, A. *et al.* (1989) **Reproductive success of females limited by males in two pipefish species**, *Am. Nat.* 133, 506–516
- Vincent, A. *et al.* (1994) **Operational sex ratios and behavioural sex differences in a pipefish population**, *Behav. Ecol. Sociobiol.* 34, 435–442
- Ahnesjö, I. (1995) **Temperature affects male and female potential reproductive rates differently in the sex-role reversed pipefish *Syngnathus typhle***, *Behav. Ecol.* 6, 229–233
- Kvarnemo, C. (1994) **Temperature differentially affects male and female reproductive rates in the sand goby: consequences for operational sex ratio**, *Proc. R. Soc. London Ser. B* 256, 151–156
- Kvarnemo, C. (1996) **Temperature affects operational sex ratio and intensity of male–male competition – an experimental study of sand gobies, *Pomatoschistus minutus***, *Behav. Ecol.* 7, 208–212
- Trivers, R.L. (1972) **Parental investment and sexual selection**, in *Sexual Selection and the Descent of Man, 1871–1971* (Campbell, B.G., ed.), pp. 136–179, Aldine
- Clutton-Brock, T.H. (1991) *The Evolution of Parental Care*, Princeton University Press
- Evans, R.M. (1990) **The relationship between parental input and investment**, *Anim. Behav.* 39, 797–798
- Knapp, R.W. (1984) **Parental investment: the problem of currency**, *Can. J. Zool.* 62, 2673–2674
- Parker, G.A. and Simmons, L.W. (1996) **Parental investment and the control of sexual selection: predicting the direction of sexual competition**, *Proc. R. Soc. London Ser. B* 263, 315–321
- Almada, V.C. *et al.* (1995) **Courting females: ecological constraints affect sex roles in a natural population of the blennioid fish *Salaria pavo***, *Anim. Behav.* 49, 1125–1127
- Vincent, A. *et al.* (1992) **Pipefishes and seahorses: are they all sex role reversed?** *Trends Ecol. Evol.* 7, 237–241
- Colwell, M.A. and Oring, L.W. (1988) **Sex ratios and intrasexual competition for mates in a sex-role reversed shorebird, Wilson's phalarope (*Phalaropus tricolor*)**, *Behav. Ecol. Sociobiol.* 22, 165–173
- Grant, J.W.A. *et al.* (1995) **Operational sex ratio, mediated by synchrony of female arrival, alters the variance of male mating success in Japanese medaka**, *Anim. Behav.* 49, 367–375
- Jormalainen, V. *et al.* (1994) **Male choice and male–male competition in *Idotea baltica* (Crustacea, Isopoda)**, *Ethology* 96, 46–57
- Enders, M.M. (1993) **The effect of male size and operational sex ratio on male mating success in the common spider mite, *Tetranychus urticae* Kock (Acari: Tetranychidae)**, *Anim. Behav.* 46, 835–846
- Kvarnemo, C. *et al.* (1995) **Effects of sex ratio on intra- and intersexual behaviour in sand gobies**, *Anim. Behav.* 50, 1455–1461
- Pitnick, S. (1993) **Operational sex ratios and sperm limitation in populations of *Drosophila pachea***, *Behav. Ecol. Sociobiol.* 33, 383–391
- Krupa, J.J. and Sih, A. (1993) **Experimental studies on water strider mating dynamics: spatial variation in density and sex ratio**, *Behav. Ecol. Sociobiol.* 33, 107–120

- 32 Arnqvist, G. (1992) **The effects of operational sex ratio on the relative mating success of extreme male phenotypes in the water strider *Gerris odontogaster* (Zett.) (Heteroptera; Gerridae)**, *Anim. Behav.* 43, 681–683
- 33 Smith, C. and Wootton, R.J. (1995) **The effect of brood cannibalism on the operational sex ratio in parental teleost fishes**, *Rev. Fish Biol. Fish.* 5, 372–376
- 34 Berglund, A. and Rosenqvist, G. (1993) **Selective males and ardent females in pipefishes**, *Behav. Ecol. Sociobiol.* 32, 331–336
- 35 Forsgren, E. *et al.* (1996) **Modes of sexual selection determined by resource abundance in two sand goby populations**, *Evolution* 50, 646–654
- 36 Madsen, T. and Shine, R. (1993) **Temporal variability in sexual selection acting on reproductive tactics and body size in male snakes**, *Am. Nat.* 141, 167–171
- 37 Höglund, J. *et al.* (1993) **Costs and consequences of variation in the size of ruff leks**, *Behav. Ecol. Sociobiol.* 32, 31–39
- 38 Summers, K. (1992) **Dart-poison frogs and the control of sexual selection**, *Ethology* 91, 89–107
- 39 Owens, I.P.F. *et al.* (1994) **Extraordinary sex roles in the Eurasian dotterel: female mating arenas, female–female competition, and female mate choice**, *Am. Nat.* 144, 76–100
- 40 Parker, G.A. (1983) **Mate quality and mating decisions**, in *Mate Choice* (Bateson, P., ed.), pp. 141–166, Cambridge University Press
- 41 Berglund, A. (1994) **The operational sex ratio influences choosiness in a pipefish**, *Behav. Ecol.* 5, 254–258
- 42 Souroukis, K. and Murray, A.-M. (1995) **Female mating behavior in the field cricket, *Gryllus pennsylvanicus* (Orthoptera: Gryllidae) at different operational sex ratios**, *J. Insect. Behav.* 8, 269–279
- 43 Grant, J.W.A. *et al.* (1995) **Mate choice by Japanese medaka (Pisces, Oryziidae)**, *Anim. Behav.* 50, 1425–1428
- 44 Cox, C.R. and LeBoeuf, B.J. (1977) **Female incitation of male competition: a mechanism in sexual selection**, *Am. Nat.* 111, 317–335
- 45 Johnstone, R.A. *et al.* **Mutual mate choice and sex differences in choosiness**, *Evolution* (in press)
- 46 Crowley, P.H. *et al.* (1991) **Mate density, predation risk, and the seasonal sequence of mate choices: a dynamic game**, *Am. Nat.* 137, 567–596

Plant physiological ecology of tropical forest canopies

Stephen S. Mulkey, Kaoru Kitajima and S. Joseph Wright

Over half of the global annual net primary production is estimated to occur in the tropics, with most of the production attributable to tropical forest¹. The canopy is the business end of tropical forest, and plant physiologists have long had great interest in understanding the ecological and physiological determinants of canopy exchange processes. Until recently, data have been sketchy, owing to the difficulty of repeated, non-destructive, *in situ* measurements in the canopy. Over the past few years, there has been a surge of work facilitated by flexible canopy access systems, such as construction (canopy) cranes and expanded walkways², as well as by advances in portable analytical equipment. Now, it is possible to examine rigorously variation in leaf exchange rates of carbon (C) and water in tropical forest canopies at contrasting spatial scales. The perspective provided by data from different scales permits a comprehensive assessment of functional diversity in the canopy, and its role in ecosystem exchange processes.

The diversity of functional characters is high in tropical forest because of the high diversity of life forms and species, and their varied responses to environmental variation. Although the growing season is not limited by low tempera-

Mechanistic information about tropical canopy function is emerging at the leaf, tree, stand and landscape levels. With improved canopy access, comprehensive data are accumulating about seasonal and spatial variation in light, temperature and humidity, and corresponding variation in leaf carbon gain and water loss.

At the whole-plant level, simultaneous measurements at different spatial scales have revealed the role of boundary layer dynamics in regulating transpiration. Emergent properties of canopy function are being explored through models that integrate leaf and landscape-level exchange processes. Integration of exchange processes that include functional diversity at different scales has the potential to validate regional estimates of gas exchange, which are critical to our understanding of the role of tropical forests in global atmospheric carbon balance.

Stephen Mulkey is at the Dept of Biology, University of Missouri – St Louis, St Louis, MO 63121-4499, USA; Kaoru Kitajima and Joseph Wright are at the Smithsonian Tropical Research Institute, Unit 0948, APO AA, Miami, FL 34002-0948, USA.

ture, strong seasonality in rainfall and light is common in tropical forests. A high diversity of leaf longevities and production strategies results in part from the contrasting seasonality of water and light availability (the rainy season is typically cloudy while light is abundant during the dry season, Fig. 1). Relative to temperate and boreal forests, tropical forests have the highest solar radiation and heat load per area due to higher solar declination. Accordingly, resource gradients within the canopy can be quite steep, especially during the dry season³. Thus, the central problem for the study of the ecophysiology of tropical canopies is to characterize often extreme spatial and temporal variation in exchange processes in a fashion that permits meaningful generalizations. Here, we review recent advances at different spatial scales of observation, with particular emphasis on the impact of the unique ecological variation of tropical forest on gas exchange in the canopy.

Canopy water relations

Seasonality of water availability and phenology

Seasonal drought constrains the productivity of tropical plants whenever water deficits are sufficient to limit