

Evolution and Development of Sex Differences in Cooperative Behavior in Meerkats

T. H. Clutton-Brock,^{1*} A. F. Russell,¹ L. L. Sharpe,² A. J. Young,¹ Z. Balmforth,³ G. M. McIlrath³

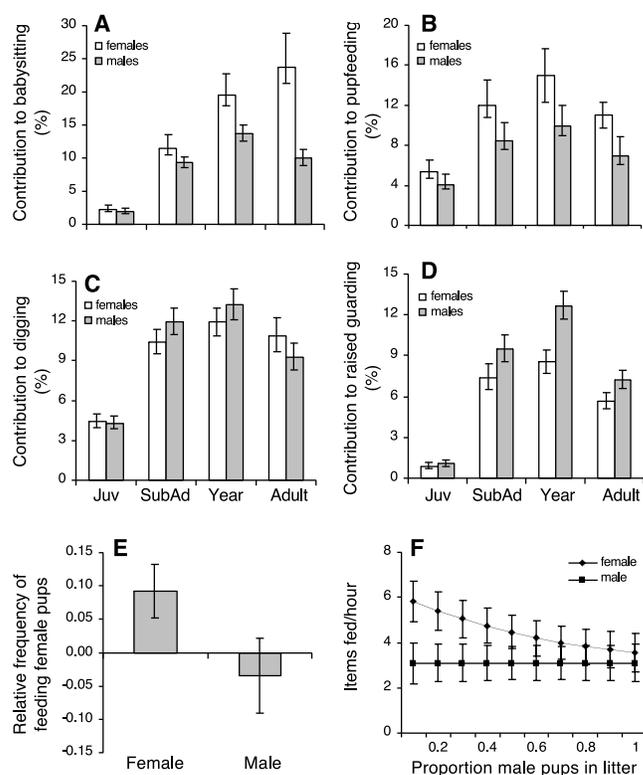
In cooperatively breeding birds, where helpers of both sexes assist with the provisioning and upbringing of offspring who are not their own, males tend to contribute more than females to rearing young. This sex difference has been attributed to paternity uncertainty, but could also occur because males contribute more where they are likely to remain and breed in their group of origin. In contrast to most birds, female meerkats (*Suricata suricatta*) are more likely to breed in their natal group than males. We show that female meerkat helpers contribute more to rearing young than males and that female helpers feed female pups more frequently than males. Our results suggest that sex differences in cooperative behavior are generated by sex differences in philopatry and occur because females derive greater direct benefits than males from raising recruits to their natal group. These findings support the view that direct, mutualistic benefits are important in the evolution of specialized cooperative behavior.

In cooperative birds, in which nonbreeding helpers of both sexes assist breeding adults rear young, male helpers commonly contribute more than females (1, 2). Two main explanations for this difference exist (2). First, male helpers may contribute more than females because wherever paternity certainty is <1 and males cannot be certain they have fathered their partner's offspring but can identify their maternal siblings (sibs), their relatedness to their sibs $[(1 + p^2)/4]$, where p is the proportion of their mate's offspring that males father, may be higher than to their offspring ($p/2$). In contrast, female helpers are, on average, more closely related to their offspring ($r = 0.5$) than to their sibs ($r = <0.5$) (2). Second, male helpers may invest more than females in avian societies because males commonly remain and breed in their group of origin, whereas females usually disperse to breed (3). Where the survival and eventual breeding success of helpers increases with group size, males may gain larger direct benefits than females from rearing additional group members in their group of origin.

Sex differences in helping behavior in cooperative mammals provide an opportunity to test these explanations. In contrast to birds, males usually disperse to breed in other groups, whereas some females remain in their natal group throughout their lives (3). Here,

we describe the development of sex differences in the level of contributions to four different cooperative activities in wild groups of meerkats (*Suricata suricatta*) in the south-

Fig. 1. Age-related changes in percentage contributions by male and female helpers to (A) babysitting, (B) pup feeding, (C) social digging, and (D) raised guarding. The level of contributions differed significantly between sexes for all activities except digging. (A) Females contributed more to babysitting than males in all age categories (juveniles, $\chi^2 = 0.27$, $df = 1$, $P = 0.61$; subadults, $\chi^2 = 4.41$, $df = 1$, $P = 0.038$; yearlings, $\chi^2 = 12.75$, $df = 1$, $P < 0.001$; adults, $\chi^2 = 32.05$, $df = 1$, $P < 0.0001$). (B) Females contributed more to pup feeding than males in all categories (juveniles, $\chi^2 = 4.64$, $df = 1$, $P = 0.031$; subadults, $\chi^2 = 14.45$, $df = 1$, $P < 0.001$; yearlings, $\chi^2 = 17.11$, $df = 1$, $P < 0.001$; adults, $\chi^2 = 15.51$, $df = 1$, $P < 0.001$). (C) Males and females did not differ in their contributions to social digging in any category (all P values > 0.2). (D) Males contributed more to raised guarding than females in all age categories except juveniles (juveniles, $\chi^2 = 0.12$, $df = 1$, $P = 0.73$; subadults, $\chi^2 = 6.06$, $df = 1$, $P = 0.014$; yearlings, $\chi^2 = 16.78$, $df = 1$, $P < 0.001$; adults, $\chi^2 = 5.24$, $df = 1$, $P = 0.022$). Last two plots show sex differences in contributions to pup feeding according to pup sex (E) and litter sex ratio (F). (E) Female helpers fed female pups more frequently than male pups, but male helpers showed no preference ($\chi^2 = 4.04$, $df = 1$, $P = 0.045$); see (13). (F) Female helpers contributed more to feeding litters that were female biased ($\chi^2 = 5.21$, $df = 1$, $P = 0.021$), but males did not ($\chi^2 = 0.13$, $df = 1$, $P = 0.72$).



ern Kalahari by using a combination of long-term field observations and experiments on 16 different habituated groups (4). Meerkats are obligately cooperative: they live in stable groups of 2 to 30 individuals, including a dominant male and female which are the parents of most of the pups born in the group, and an approximately equal number of helpers of both sexes (5). Males and females are similar in weight. Both sexes approach adult weight and foraging success by the middle of their second year of life, although they continue to gain weight over their life-span (fig. S1). Some females breed as subordinates in their natal group, whereas males rarely or never do so, though older natal males often spend a proportion of their time roving in search of females outside their natal group ("prospecting") (4). Most females are ejected from their natal group in their second or third year of life by the dominant breeding female, whereas males leave voluntarily to disperse to other breeding groups or to establish new ones at similar ages (6). Females typically disperse in single-sex parties of two to six; males most frequently disperse individually. Most helpers are animals that have not yet dispersed from their natal group. Therefore, to ensure comparability, our analyses are re-

¹Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK. ²Department of Zoology, University of Stellenbosch, Matieland 7602, Republic of South Africa. ³Mammal Research Institute, University of Pretoria, 0002 Pretoria, Republic of South Africa.

*To whom correspondence should be addressed. E-mail: thcb@hermes.cam.ac.uk

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Fig. 2. Effects of body weight on contributions by male and female helpers less than 1 year old to (A) babysitting, (B) pup feeding, (C) social digging, and (D) raised guarding. Heavy females contributed significantly more than light females to babysitting ($\chi^2 = 4.91$, $df = 1$, $P = 0.027$) and pup feeding ($\chi^2 = 6.86$, $df = 1$, $P = 0.009$), whereas heavy males contributed significantly more than light males only to raised guarding ($\chi^2 = 6.23$, $df = 1$, $P = 0.013$). The last two plots show the effects of experimental feeding of pups during peak provisioning on their subsequent contributions to (E) babysitting and (F) pup feeding. Males and females differed in the effects of feeding on their contributions to babysitting ($\chi^2 = 5.38$, $df = 1$, $P = 0.023$) and pup feeding ($\chi^2 = 7.42$, $df = 1$, $P = 0.006$), but no helper sex or feeding treatment interactions were found in contributions to digging ($\chi^2 = 0.01$, $df = 1$, $P = 0.91$) or raised guarding ($\chi^2 = 1.74$, $df = 1$, $P = 0.19$).

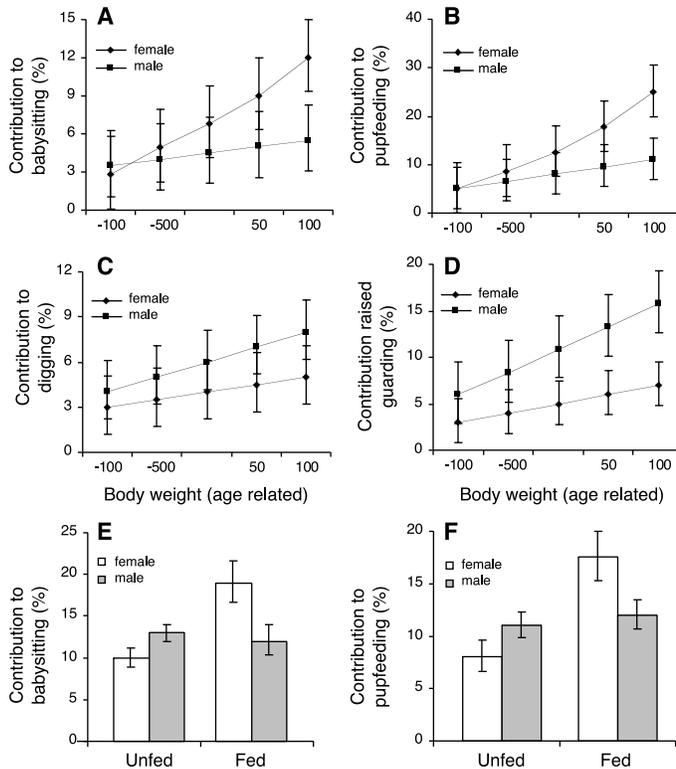
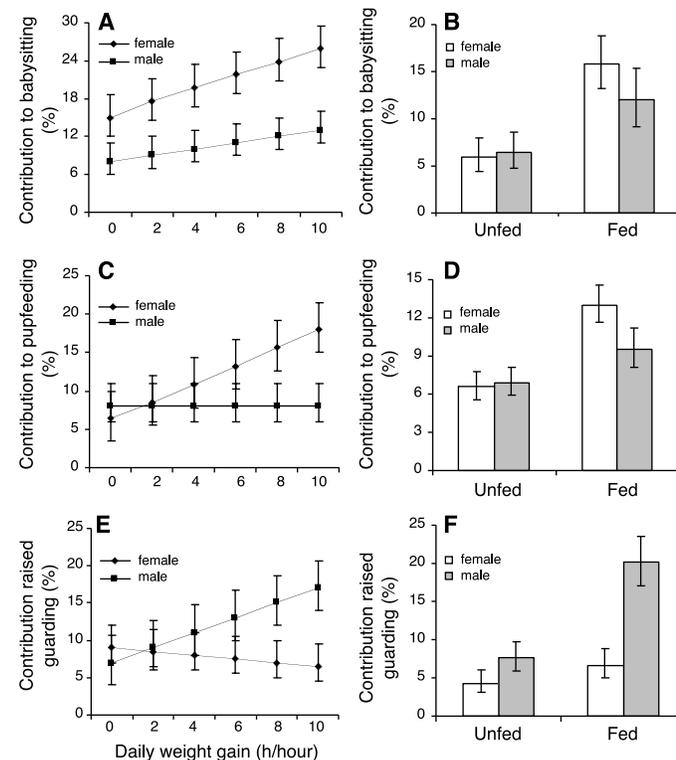


Fig. 3. Effect of daily weight gain (g/hour) on contributions by male and female helpers over 1 year old to (A) babysitting, (C) pup feeding, and (E) raised guarding. In females, daily weight gain affected contributions to babysitting ($\chi^2 = 3.28$, $df = 1$, $P = 0.070$), pup feeding ($\chi^2 = 4.64$, $df = 1$, $P = 0.031$), and digging ($\chi^2 = 6.20$, $df = 1$, $P = 0.013$) but not to raised guarding ($\chi^2 = 0.41$, $df = 1$, $P = 0.52$). In males, daily weight gain affected only contributions to digging ($\chi^2 = 8.62$, $df = 1$, $P = 0.003$) and raised guarding ($\chi^2 = 5.09$, $df = 1$, $P = 0.024$). Effects of experimental feeding of helpers on their contributions to (B) babysitting, (D) pup feeding, and (F) raised guarding in the same breeding event. Experimental feeding raised contributions by females to babysitting ($\chi^2 = 15.89$, $df = 1$, $P < 0.001$), pup feeding ($\chi^2 = 6.47$, $df = 1$, $P = 0.011$), and digging ($\chi^2 = 14.89$, $df = 1$, $P < 0.001$), and contributions by males to babysitting ($\chi^2 = 14.59$, $df = 1$, $P < 0.001$) and digging ($\chi^2 = 15.03$, $df = 1$, $P < 0.001$). In contrast, feeding did not affect female contributions to raised guarding ($P > 0.5$), but it increased contributions by males ($\chi^2 = 11.33$, $df = 1$, $P = 0.001$).



stricted to helpers living in their natal group.

Helpers of both sexes contribute to four distinct cooperative activities: “babysitting” pups of 1 to 3 weeks at the natal burrow; feeding pups of 1 to 3 months with invertebrates and small vertebrates (“pup feeding”); clearing sleeping burrows and bolt-holes of sand (“social digging”); and sentinel duty when the group is foraging (“raised guarding”). Individual contributions to most cooperative activities increase during the first 2 years of life in both sexes (Fig. 1, A to D). At most ages, female helpers contribute more to the care of young than males (Fig. 1, A and B). In contrast, contributions to digging do not differ between the sexes, (Fig. 1C) and males generally contribute more than females to raised guarding (Fig. 1D). Although these differences are apparent by the time juveniles are 6 months old, they are most pronounced among older helpers (Fig. 1, A to D). Older male helpers, in particular, tend to reduce their investment in rearing young (Fig. 1, A and B). Like differences between age categories, differences between the sexes are largest in big groups where helper/pup ratios are high (7).

Analysis of individual differences in contributions to cooperative behavior suggests that, when nutritional constraints are relaxed, female helpers increase their investment in caring for pups, whereas males increase their investment in raised guarding. In the first year of life, individual contributions to most cooperative activities are related to variation in body weight (Fig. 2, A to D). These effects vary between the sexes: heavy female helpers contribute more to babysitting and pup feeding, whereas the contributions of males to these activities are lower and are unaffected by their weight (Fig. 2, A and B). Contributions to social digging do not vary significantly with body weight in either sex are unaffected by body weight in both sexes (Fig. 2C), and contributions to raised guarding increase with body weight to a greater extent in males than in females (Fig. 2D). The different effects of body weight on males and females are confirmed by experiments in which samples of male and female pups 4 to 10 weeks old (the main period of pup feeding by helpers) had their daily food intake supplemented with 25 g of hard-boiled egg per day (fig. S2). Female pups whose daily food intake had been supplemented (“fed”) had higher body weights at 3 to 4 months and throughout the rest of their lives than nonsupplemented (“unfed”) controls, the effects of feeding on the weight of male pups disappeared by the age of 6 months (fig. S2). Fed female pups contributed more during their first year of life to babysitting and pup feeding subsequent litters than unfed female controls, whereas fed males tended to show lower contributions to babysitting and pup feeding than unfed male

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controls, generating significant interactions between sex and treatment (Fig. 2, E and F).

After helpers are a year old, variation in cooperative behavior is no longer consistently related to variation in body weight, and differences in behavior between fed and unfed pups disappear (8). Individual differences in cooperative behavior are now related to variation in daily weight gain (Fig. 3, A, C, and E), which reflects individual differences in foraging success (9). Like increased body weight in the first year of life, high daily weight gains raise contributions to babysitting and pup feeding to a greater extent in females than in males (Fig. 3, A and C) and increase contributions to sentinel duty in males but not in females (Fig. 3E). Experimental feeding of adult helpers during the period of pup care (4) significantly raises contributions to babysitting in both sexes (Fig. 3B): to pup feeding in females but not males (Fig. 3D), and to sentinel duty in males but not females (Fig. 3F).

Because coefficients of relatedness between natal male and female helpers and pups are identical (10), sex differences in contributions to cooperative activities are unlikely to be caused by differences in kinship. Female helpers may gain greater direct benefits than males from raising young in their natal group for three reasons. If females dispersed at later ages than males, they could gain increased benefits to their survival because mortality declines with increasing group size (11, 12). However, in meerkats, average age at dispersal is similar for males and females (Fig. 4A). Second, where females but not males may breed in their natal group, females may gain greater benefits to their breeding success because pup survival increases with group size (12). Males, who rarely or never breed in their natal group, derive no similar benefits. Third, females may benefit more from recruits to their natal group than males, because females usually disperse in larger parties than males, and party size is more important for dispersing females than males (4).

Male and female helpers are also likely to differ in the relative benefits they derive from raising female recruits. Because they have a higher probability of breeding in their natal group, female helpers might be expected to favor the production of heavy female recruits that are likely to contribute more to rearing young (see Fig. 2, A and B). Moreover, female helpers could gain more from rearing female recruits, because the latter may be their companions during dispersal attempts. As predicted, female helpers show a consistent preference for feeding female pups (Fig. 1E) (13) and their contributions to pup feeding increase in litters where the sex ratio is biased toward females (Fig. 1F). Male helpers show no consistent preference for feeding

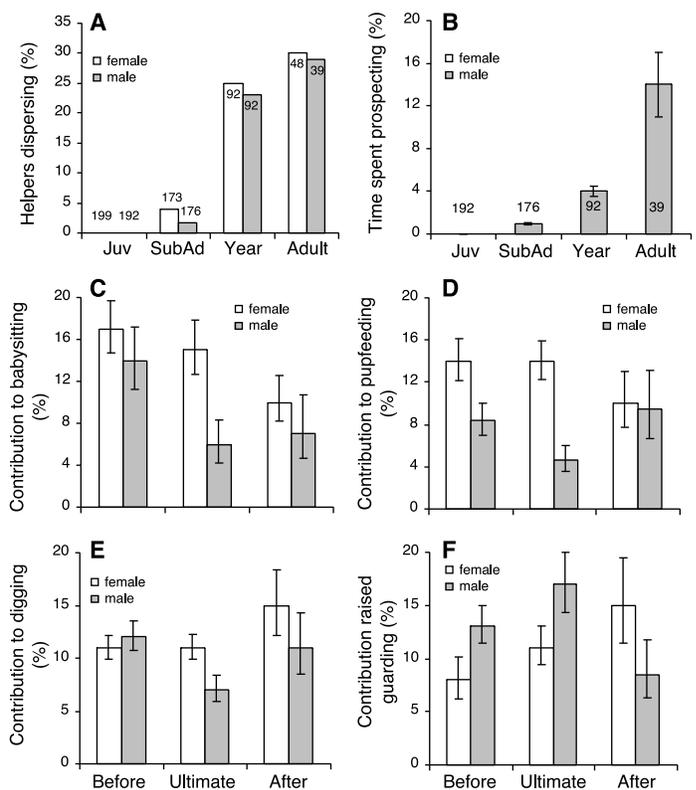
pups of either sex, and their investment in feeding pups does not change with the sex ratio of the litter.

Contributions to cooperative behavior among males are related to their proximity to dispersal (tables S1 to S4). Although male and female helpers disperse at similar ages (Fig. 4A), older male helpers spend part of their time prospecting for females outside their natal group before dispersing (Fig. 4B). As dispersal approaches, males (but not females) significantly reduce their contributions to babysitting, digging, and pup feeding (Fig. 4, C to E). Reductions in male contributions to pup rearing are not a consequence of increased time spent away from their natal group (Fig. 4B) or of reduced weight in frequent prospectors, because both are controlled for in the analyses. The most likely explanation is that, as dispersal approaches, there is a decline in the future direct benefits that males are likely to gain from raising recruits to their natal group. As expected, males increase their contributions to feeding pups after they have joined or formed a new group where they are likely to breed (Fig. 4D), though their contributions to babysitting do not change (Fig. 4C). In contrast, males increase their contributions to raised guarding shortly before dispersal and reduce them once they are members of a new group (Fig. 4F), perhaps because they are likely to benefit by

gaining information about the presence of females in other groups or in dispersing parties during the months before dispersal. The larger direct benefits that males may derive from raised guarding may also explain why their contributions to sentinel duty are generally greater than those of females (Figs. 1D, 2D, and 3E).

Existing studies of sex differences in helping behavior in cooperative vertebrates in which both sexes act as helpers in their natal group suggest that there is an association between sex differences in cooperative behavior and philopatry (2). In species like meerkats, in which females may remain and breed in their natal group (including dwarf mongooses, brown hyenas, and Seychelles warblers), female helpers appear to contribute more to rearing young than males (14–16), whereas males contribute more than females in species in which males are more likely to remain and breed in their natal group (including most cooperative birds and African wild dogs) (2, 17). In naked mole rats (*Heterocephalus glaber*), in which both males and females typically remain in their natal group, no sex differences in cooperative activities occur in “normal” helpers (18), though a minority of males adopt an alternative growth strategy that leads eventually to emigration and outbreeding and contribute little to cooperative activities (19). In con-

Fig. 4. Dispersal and contributions to cooperative behavior. (A) Proportion of helpers that dispersed in each age category. (B) Proportion of time spent by males prospecting outside their group. Effect of proximity to dispersal on contributions of helpers to (C) babysitting, (D) pup feeding, (E) social digging, and (F) raised guarding. Average contributions are shown for subordinates in the last breeding event before dispersal (Ultimate), the three breeding events preceding the ultimate breeding event (Before), and the two breeding events after dispersal to a new group (After). In no case did contributions by females change before dispersal ($P > 0.65$), whereas males reduced their contributions to babysitting ($\chi^2 = 5.67$, $df = 2$, $P = 0.059$), pup feeding ($\chi^2 = 8.93$, $df = 2$, $P = 0.012$), and digging ($\chi^2 = 8.79$, $df = 2$, $P = 0.012$) for their ultimate breeding event within their natal group and increased their contribution to raised guarding ($\chi^2 = 7.88$, $df = 2$, $P = 0.020$).



trast, contributions to sentinel duty are usually greater in males than in females, regardless of patterns of philopatry (20–23), perhaps because males gain information about the distribution of females by watching from raised positions.

Our results have three broader implications. First, they show that pronounced sex differences in behavioral development can occur in effectively monogamous species with little sexual dimorphism in body size. Differences similar to those we have described here may be expected to occur in other cooperative species. Second, our results emphasize that comparisons of cooperative behavior among helpers need to control for the effects of age, weight, sex, and nutritional status; attempts to investigate the influence of particular variables (such as kinship) on individual contributions to cooperative activities that do not control for these effects may generate misleading results. Lastly, our results suggest that differences between male and female helpers in their contributions to rearing young vary with the direct costs and benefits of cooperative activities to each sex generated by sex differences in philopatry. Previous analyses of cooperative behavior in meerkats have shown that individual differences in contributions to cooperative activities are unrelated to levels of kinship (24, 25), and our results are consistent with the suggestion that mutualistic, direct benefits play an important role in the evolution and maintenance of cooperative breeding (26).

References and Notes

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7. As group size increases, males reduce investment in babysitting to a greater extent than females (subadults, $\chi^2 = 10.08$, $df = 1$, $P = 0.002$; yearlings, $\chi^2 = 12.04$, $df = 1$, $P = 0.001$) as well as in pup feeding (subadults, $\chi^2 = 4.98$, $df = 1$, $P = 0.024$; adults, $\chi^2 = 3.35$, $df = 1$, $P = 0.067$). In contrast, in larger groups, females reduce their investment in digging (adults, $\chi^2 = 12.71$, $df = 1$, $P = 0.001$) and raised guarding (adults, $\chi^2 = 5.24$, $df = 1$, $P = 0.022$) to a greater extent than males. (For all other age categories, $P > 0.1$).
8. After the first year of life, helper contributions are not consistently related to body weight, and female helpers fed as pups do not contribute any more to cooperative activities than unfed controls ($P > 0.65$ for fed versus unfed; $P > 0.3$ for interactions between fed and unfed, males and females).
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Supporting Online Material

www.sciencemag.org/cgi/content/full/297/5579/253/DC1

Materials and Methods

Figs. S1 and S2

Tables S1 to S4

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Leg Patterning Driven by Proximal-Distal Interactions and EGFR Signaling

M. I. Galindo, S. A. Bishop, S. Greig, J. P. Couso*

wingless and *decapentaplegic* signaling establishes the proximal-distal axis of *Drosophila* legs by activating the expression of genes such as *Distalless* and *dachshund* in broad proximal-distal domains during early leg development. However, here we show that *wingless* and *decapentaplegic* are not required throughout all of proximal-distal development. The tarsus, which has been proposed to be an ancestral structure, is instead defined by the activity of *Distalless*, *dachshund*, and a distal gradient of epidermal growth factor receptor (EGFR)–Ras signaling. Our results uncover a mechanism for appendage patterning directed by genes expressed in proximal-distal domains and possibly conserved in other arthropods and vertebrates.

Animal appendages develop along a proximal-to-distal (PD) axis, from proximal body wall to distal tip. This axis is not inherited from the embryo and is established anew in each developing appendage. In *Drosophila* legs, the combination of a dorsal signal provided by the *BMP4* homolog *decapentaplegic* (*dpp*) with a ventral signal provided by the *Wnt* homolog *wingless* (*wg*) establishes the PD axis (1), in addition to organizing the dorsal-ventral appendage pattern (2, 3). Signaling from *wg* and *dpp* activates the expression of the genes *Distalless* (*Dll*) and *dachshund* (*dac*) early in leg development (4, 5). *Dll* encodes a homeodomain protein expressed and required in the distal half of the leg, from tibia to pretarsus, whereas *dac* encodes a nuclear protein expressed and required me-

dially in the femur and tibia. However, the leg comprises 10 segments along the PD axis, whose specification involves further genes (6). Here we describe how, after 84 hours of development, PD patterning becomes *wg*- and *dpp*-independent. Instead, a mechanism mediated by genes expressed in PD domains, such as *Dll*, *dac*, and the epidermal growth factor receptor (EGFR) ligand *vein*, activates the expression of further genes and generates distal leg fates such as the tarsus. Previous data in *Drosophila* and on homologous genes in other arthropods and vertebrates suggest that this PD patterning mechanism might be conserved and ancestral.

We studied the timing of *wg* requirements for PD development with a temperature-sensitive mutant (7). Removal of *wg* function before 72 hours after egg laying (hours AEL) produces truncated legs lacking the distal parts and showing ventral patterning defects (Fig. 1, A and B). However, shifts of animals from permissive to restrictive temperature at

School of Biological Sciences, University of Sussex, Falmer, Brighton BN1 9QC, UK.

*To whom correspondence should be addressed. E-mail: J.P.Couso@biols.susx.ac.uk