Cooperation, Control, and Concession in Meerkat Groups

T. H. Clutton-Brock,[1]* P. N. M. Brotherton,[1] A. F. Russell,[1]
M. J. O'Riain,[2] D. Gaynor,[2] R. Kansky,[2] A. Griffin,[3] M. Manser,[1]
L. Sharpe,[2] G. M. McIlrath,[2] T. Small,[4] A. Moss,[4] S. Monfort[4]

"Limited control" models of reproductive skew in cooperative societies suggest that the frequency of breeding by subordinates is determined by the outcome of power struggles with dominants. In contrast, "optimal skew" models suggest that dominants have full control of subordinate reproduction and allow subordinates to breed only when this serves to retain subordinates' assistance with rearing dominants' own litters. The results of our 7-year field study of cooperative meerkats, *Suricata suricatta*, support the predictions of limited control models and provide no indication that dominant females grant reproductive concessions to subordinates to retain their assistance with future breeding attempts.

Meerkats (or suricates) live in groups of 2 to 30 adults, subadults, and juveniles in arid areas of southern Africa (*1*). They are obligate cooperative breeders: All adult group members contribute to guarding and feeding young, and the growth rate and survival of pups increase in relation to the number of animals in the group (*1–5*). Over the past 7 years, we have monitored the reproductive success of over 400 individually identifiable animals belonging to more than 20 different free-ranging groups, using a combination of observation, field experiments, and DNA microsatellite analysis (*1*, *6*). All meerkat groups include a dominant female, who is usually the oldest and heaviest female in the group (*7*) and who is the mother of around 80% of the litters born in her group, as well as a dominant male who fathers over 80% of her offspring (*6*). In groups including more than one adult female, dominant females give birth to an average of 2.8 litters per year each, as compared to 0.9 litters per year for each adult subordinate female (Wilcoxon test: $t = 55$, $n = 10$, $P < 0.01$).

The low breeding frequency of subordinate females does not occur because they are incapable of breeding, as is the case in some cooperative mammals (*8*). Dominant and subordinate adult females show similar luteinizing hormone responses to experimental challenge with gonadotropin-releasing hormone (GnRH), which indicates that they are physiologically capable of breeding (*9*), although levels of estrogen metabolites in feces are lower in subordinates than in dominants (Mann-Whitney U test: $Z = 1.98$, $P = 0.05$; Fig. 1A) (*10–12*). As in some cooperative birds (*13*), inbreeding avoidance contributes to the lower frequency of breeding by subordinates. Many subordinate females live in groups that contain no males unrelated to them. These animals show lower levels of fecal estrogen (Sign test on median values, $P < 0.002$; Fig. 1B) (*10*) and are less likely to breed ($P < 0.03$; Table 1 and Fig. 1C) (*14*) than are subordinates living in groups including unrelated males. Subordinates living in groups without unrelated males commonly mate with roving males from other groups (*6*) and are clearly capable of breeding, although dominant females may more easily restrict their access to mates.

The distribution of breeding by subordinates matches the prediction of "limited control" models of subordinate reproduction (*15*, *16*) that subordinates should be most likely to breed where the dominant's capacity for control is reduced or the net benefits of breeding to subordinates are high. Immediately after a new female succeeds to the dominant position, her capacity to dominate other group members is reduced, and the incidence of subordinate breeding is substantially higher in her first 3 months as dominant than at other times (Kruskal Wallis test, $H = 11.25$, df = 3, $P = 0.01$; Fig. 2A) (*17*). Subordinate breeding is more frequent when the benefits of breeding to subordinates are relatively high (Fig. 1C) or the costs are low. For example, subordinates more frequently breed in seasons of high rainfall (Table 1), when food is abundant and all group members are in relatively good condition, whereas rainfall

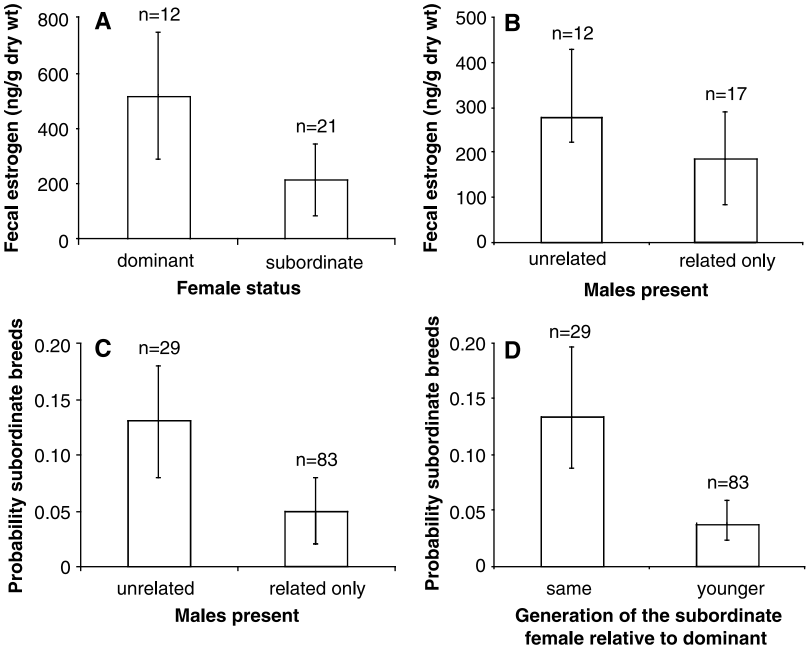

Fig. 1. (**A**) Median levels of estrogen metabolites (±interquartile ranges) in fecal samples from nonpregnant dominant and subordinate adult females during the breeding season (*10*). (**B**) Median levels of estrogen metabolites (±interquartile ranges) in fecal samples collected from subordinate females of breeding age (>10 months old) in groups with and without unrelated males (*10*). (**C**) Annual probability that subordinate females will breed in the presence and absence of unrelated males when other factors are controlled (see Table 1) [the graph shows the back-transformed means (±SE) predicted from the GLMM described in Table 1]. (**D**) Probability of breeding by subordinate females from the same generation (sibling or littermate) as the dominant versus from a different generation (daughter or niece) from the dominant (from Table 1). The graph shows the back-transformed mean predicted values (±SE) from the GLMM described in Table 1. In all (A) through (D), *n* refers to the number of females sampled.

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[1] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK. [2] Mammal Research Institute, University of Pretoria, 0002 Pretoria, South Africa. [3] Institute of Cell, Animal and Population Biology, University of Edinburgh, King's Buildings, West Mains Road, Edinburgh EH9 3JT, UK. [4] Conservation and Research Center, Smithsonian Institution, 1500 Remount Road, Front Royal, VA 22630, USA.

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

has no significant effect on the frequency of reproduction by dominants (*18*). Breeding is also commonest among those categories of subordinate that the dominant female is likely to find most difficult to control. Heavier subordinates are more likely to breed than lighter ones ($P < 0.001$; Table 1 and Fig. 2B). And, when the effects of weight and access to unrelated males are controlled, subordinates that are of the same generation as the dominant female (whether they are full sibs or half sibs) are more likely to breed than subordinates that are members of the next generation (whether they are daughters or nieces) ($P < 0.03$; Table 1 and Fig. 1D). Because dominance is age-related (*1*), the effects of generation are likely to occur because dominant females can more easily control animals of the next generation (which have been subordinate to them throughout their lives) than members of their own generation.

Although these results are consistent with the predictions of limited control models, they do not specifically reject those of "optimal skew" models (*15*, *19*). The latter assume that dominant females have full control of subordinate reproduction and predict that they should allow subordinates to breed when the benefits of retaining them in the group exceed the costs of allowing them to breed. However, the assumptions of optimal skew models may not apply in many vertebrate societies. In meerkats and in several other cooperative mammals, dominant females do not appear to have full control of subordinate reproduction. In addition, subordinate females rarely leave their natal group voluntarily and are usually driven out by the dominant female, and individuals that have bred are no less likely to disperse (Table 2) (*20*) or to assist with babysitting or pup feeding (Fig. 2C) than are those that have not bred (Wilcoxon tests: $P = 0.83$, $P = 0.21$). Finally, it seems unlikely that the benefits of retaining one helper in the group exceed the costs of allowing an additional female to breed, for the addition of pups to litters reduces the daily weight gain of all pups, which is related to their survival (*1*, *5*).

Nor does the distribution of subordinate breeding in meerkats match the usual predictions of optimal skew models (*15*, *19*). If dominants allow subordinates to breed to retain their assistance, subordinate breeding should be most frequent in small groups, because the strong relationship between group size and survival that exists in groups of ≤11 animals (*1*) disappears once groups have exceeded this size (*21*). However, there is no association between group size and the frequency of subordinate breeding, which is as high in groups of more than 11 animals as in smaller ones (Table 1). There is also no significant relationship between the probability that individual subordinates will disperse and their frequency of breeding. For example, although older subordinates are more likely to disperse than younger ones, they are less likely to breed in their natal group. Similarly, although heavy subordinates are more likely to breed than lighter ones, they are no more likely to disperse (Tables 1 and 2).

Optimal skew models also predict that dominants should allow unrelated or distantly related group members to breed more frequently than close relatives, because the former will gain few indirect benefits from the dominant's breeding attempts and so should be more likely to disperse (*15*, *19*). This is not the case in meerkats. Although the sisters of the dominant female tend to breed more frequently than their daughters (as some optimal skew models predict), there is no

Table 1. Generalized linear mixed model of the factors affecting breeding by subordinate females (*14*).

Model term	Wald statistic (χ^2)	df	P
Rainfall (category)	28.24	2	<0.001
Weight	14.67	1	<0.001
Age (category)	13.68	3	0.003
Presence of unrelated male	5.14	1	0.023
Generation	4.83	1	0.028
Relatedness	3.05	1	0.081
Study site	1.47	1	0.23
Dominant female age	1.31	1	0.25
Number of adult females	0.99	1	0.77
Group size (category)	0.09	3	0.80
Minimal model	**Average effect**		**SE**
Constant	−3.99		0.83
Rainfall			
0–50 mm	0		0.41–0.62
51–100 mm	3.18		
>100 mm	3.05		
Weight	0.16		0.0041
Age			
<12 months	0		0.67–1.32
1–2 years	−0.28		
3–4 years	−2.60		
>4 years	−3.45		
Unrelated male (present > absent)	1.12		0.50
Generation (same > next)	1.30		0.59

Table 2. Generalized linear mixed model of the factors affecting temporary (model A) and permanent (model B) dispersal by subordinate females (*20*).

Model term	Wald statistic (χ^2)	df	P
Model A			
Age (category)	18.66	2	<0.001
Number of females	1.04	1	0.31
Presence of unrelated male	0.46	1	0.50
Breeding history	0.03	1	0.87
Model B			
Age (category)	5.51	2	0.06
Breeding history	2.34	1	0.13
Number of females	1.44	1	0.23
Presence of unrelated male	0.79	1	0.37
Minimal model	**Average effect**		**SE**
Constant	0.95		0.42
Age			
9–12 months	0.00		0.61–1.15
1–2 years	1.68		
>2 years	4.70		

significant effect of relatedness on breeding frequency, and the trend shown in Table 1 is in the opposite direction.

Because dominant females sometimes kill pups born to subordinates during their first days of life (*22*), they could encourage some subordinate females to remain in the group by systematically sparing their pups. Analysis of the survival of pups born to subordinates provides no support for this suggestion (*23*). The probability that pups born to subordinates survive to emergence from the breeding burrow is not significantly related to the number of helpers present in the group or to their mother's age (*5*, *22*). The reproductive status of the dominant female is the only factor obviously associated with the survival to emergence of pups born to subordinates: Some pups survive to emergence in only 15% of litters born to subordinates when the dominant female is pregnant (Fig. 2D), whereas some pups survive to emergence in 63% of litters born to subordinates after the birth of the dominant's offspring ($\chi^2 = 11.38$, df = 1, $P = 0.001$) (Fig. 2D). This difference probably occurs because pups born to subordinates before the dominant gives birth are more dangerous competitors to her pups than those born later. After pups have emerged, infanticide by other members of the same group has never been observed.

Our results provide an opportunity to test the assumptions and predictions of optimal skew models in cooperative vertebrates. They indicate that subordinate female meerkats are most likely to breed when they have regular access to unrelated males and control by the dominant female is weak, or when they are well placed to resist suppression. There is no indication that subordinate females that have bred are less likely to disperse or more likely to provide extra care. And, contrary to the usual predictions of optimal skew models (*15*, *19*), there is no indication that subordinates are more likely to breed when their presence is most likely to increase the fitness of the dominant female, when they are most likely to disperse, or when they are distantly related to the dominant female.

Although studies of females in several other vertebrates have been cited as providing evidence supporting optimal skew models (*15*, *19*), their results are open to the alternative interpretation that subordinates breed when dominants are unable to control them (*16*). It is, of course, possible to modify the usual predictions of optimal skew models to suggest that dominants grant reproductive concessions to subordinates that they are unable to control. However, if dominant females do not have full control of subordinates, the simplest explanation of subordinate reproduction is that subordinates breed when dominants cannot control them. Arguments that some more complex process is involved and that dominants make adaptive concessions to subordinates to retain them in the group need to show (i) that subordinates breed when dominants modify their behavior to allow them to do so and (ii) that subordinates that are allowed to breed are more likely to stay and assist with rearing the dominant's offspring. As yet, there is no firm evidence that this is the case in vertebrate societies (*16*), and it is uncertain whether optimal skew models offer realistic explanations of breeding by subordinate females.

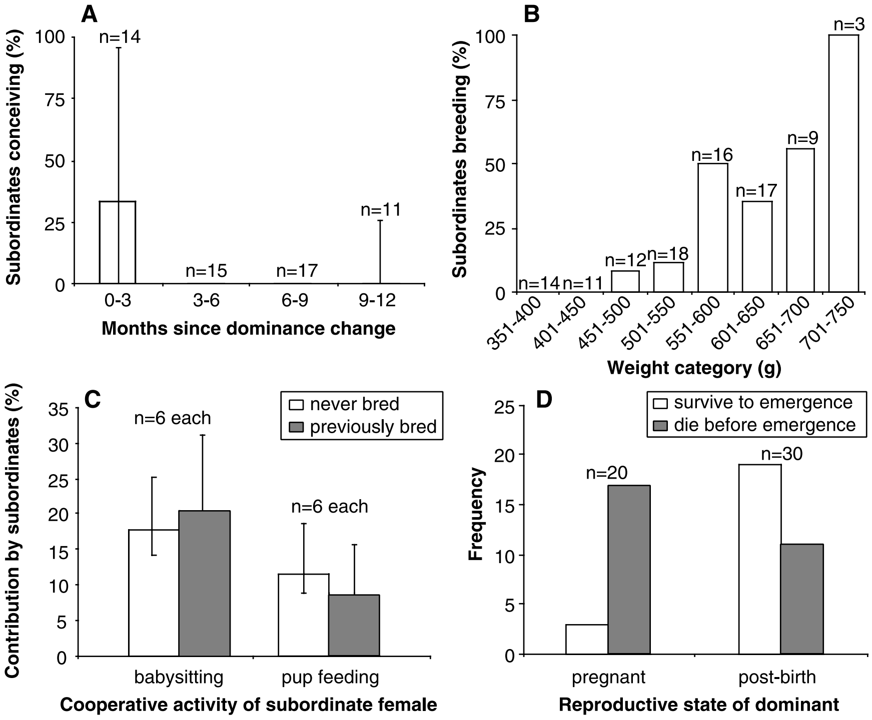

Fig. 2. (**A**) Percentage of subordinate females (over 10 months old) that conceived in each 3-month period after a change in the identity of the dominant female. The graph shows medians ± interquartile ranges; *n* refers to the number of groups. (**B**) Percentage of subordinate females of each weight category breeding per year. For each female, the average (nonpregnant) weight across the breeding season (October to April) was calculated, and this was related to whether or not she bred in that season; *n* refers to the number of subordinate females in each weight category. Females included in this sample were weighed at dawn on at least 10 occasions by inducing them to stand on electronic balances. (**C**) Relative helping contributions (expressed as percentage contributions by all group members) by adult subordinate females that had, and had not, previously bred in their natal group. Relative babysitting contributions were calculated using the total number of sessions during which each individual guarded the pups across the babysitting period (approximately 4 weeks) [see (*2*) and (*4*) for details of methods]. For pup feeding, the average daily proportion of feeds contributed by each individual was calculated over the first 40 days that the pups accompanied the group. The graph shows medians (±interquartile ranges), and *n* refers to the number of groups sampled. (**D**) Frequency of survival to emergence versus death before emergence of litters born to subordinate females when the dominant female was pregnant and after she had given birth (*23*). *n* refers to the number of litters.

References and Notes

1. T. H. Clutton-Brock *et al.*, *J. Anim. Ecol.* **68**, 672 (1999).
2. T. H. Clutton-Brock *et al.*, *Proc. R. Soc. London Ser. B* **265**, 185 (1998).
3. S. P. Doolan, D. W. Macdonald, *J. Ethol.* **105**, 851 (1999).
4. P. N. M. Brotherton *et al.*, *Behav. Ecol.*, in press.
5. T. H. Clutton-Brock, unpublished data.
6. A. S. Griffin, thesis, Edinburgh University (1999).
7. Pregnancy can be reliably detected from the fourth week after conception. In all 14 groups where the age of the dominant female was known precisely, the dominant was the oldest female of the group, and in over 90% of the groups the dominant female was also the heaviest. The weights of 10 dominant females averaged 789.3 ± 30.2 g, as compared to 659.8 ± 21.6 g for adult female subordinates (>12 months old) in the same group ($t = 4.72$, $n = 13$, $P < 0.001$) [see (*24*)].
8. C. G. Faulkes, D. H. Abbott, in *Cooperative Breeding in Mammals*, N. G. Solomon, J. A. French, Eds. (Cambridge Univ. Press, Cambridge, 1997), pp. 268–301.
9. M. J. O'Riain, N. C. Bennett, P. N. M. Brotherton, *Behav. Ecol. Sociobiol.*, in press.
10. Estrogen metabolites were measured in 5- to 10-g samples of dried feces collected from individual animals during the breeding season, using assay techniques developed for other carnivores by S. P. Monfort (*11*) and modified and validated for meerkats (*12*). Estimates of relative levels of fecal metabolites were analyzed with a residual maximum likelihood model based on 91 samples from 29 individuals in 12 groups [see (*24*)].
11. S. L. Monfort, N. P. Arthur, D. E. Wildt, *J. Reprod. Fertil.* **91**, 155 (1991).
12. A. Moss, thesis, George Mason University, Fairfax, VA (2000).
13. W. D. Koenig, J. Haydock, M. T. Stanback, *Am. Nat.* **151**, 243 (1998).
14. To investigate the factors affecting breeding by subordinates, we constructed a generalized linear mixed model (GLMM) using breeding data from 109 subor-

dinate females in 13 groups [see (*24*)]. For each 3-month period, we scored whether or not each female conceived (3 months is close to the minimum interbirth interval) and fitted these data to a binomial distribution. Weight was calculated as the mean of all morning weights for each female during each 3-month period (excluding weights during pregnancy). Generation was defined relative to the dominant: littermates and siblings were considered to be of the same generation; daughters and nieces were allocated to the next generation. Relatedness was calculated from each helper to the pups it cared for using pedigrees derived from microsatellite analysis (*6*) and was a direct measure of consanguinity (0.5 for full sibs, 0.25 for half sibs and grand-offspring, 0.25 or 0.125 for aunts, and 0.125 or 0.0612 for cousins). Group sizes were categorized as 2 to 6, 7 to 11, 12 to 16, and >16 members (excluding pups). Rainfall, weight, age category, generation relative to the dominant, and the presence of unrelated males all had a positive significant effect on the probability of a subordinate conceiving in any 3-month period. Subordinate breeding was less common when rainfall was 0 to 50 mm than for 51 to 100 mm or >100 mm. Though age and weight are closely correlated ($r = 0.72$, $n = 350$, $P < 0.001$), our analysis showed that for a given weight, subordinate females under 2 years old were more likely to breed than were older subordinates.

15. H. K. Reeve, S. T. Emlen, L. Keller, *Behav. Ecol.* **9**, 267 (1998).
16. T. H. Clutton-Brock, *Trends Ecol. Evol.* **13**, 288 (1998).
17. Our analysis compares the proportion of subordinate females that became pregnant 0 to 3, 3 to 6, 6 to 9, and 9 to 12 months after a change in the identity of the dominant female, with the expected number of conceptions occurring within 10 days of the previous conception, calculated on the assumption that subordinate conceptions were randomly distributed throughout the breeding season (from August to May).
18. Rainfall has no significant effect on the probability that dominants will breed in any 3-month period ($\chi^2 = 4.68$, df = 2, $P = 0.12$) [see (*24*)].
19. L. Keller, H. K. Reeve, *Trends Ecol. Evol.* **9**, 98 (1994).
20. To investigate the factors influencing dispersal by subordinate females, we constructed two GLMMs using data from 59 females in 11 groups involving 33 dispersal events. In model A, we used all instances of dispersal (whether or not they were permanent) and scored whether each female dispersed or stayed in the group. Dispersal events within a week of each other were not considered to be separate. In model B, we considered only females that left the group permanently. In each case, the data were fitted to a binomial model, and the dispersal event was fitted as a random term because of repeated sampling of individuals. Only females of breeding age (over 10 months) were included. "Breeding history" incorporated two categories reflecting whether or not females had bred previously in their natal group. The significant term in model A was age (older individuals were more likely to disperse than younger ones). A number of measures of group size were investigated, including all individuals over 10 months and all individuals over 6 months; only the results for the former are shown in Table 2. Group size had no significant effect on dispersal rates, and dispersal was as common in small groups as in large ones.
21. Group size (the number of individuals, excluding pups) reduces the mortality of dependent (<3 months) pups and subadults/adults (animals over 6 months old) [see (*24*)] in groups of less than 11 animals (Pearson's regressions: $T_{1,87} = -3.55$, $P <$ 0.001 for pups; $T_{1,36} = -2.29$, $P < 0.03$ for animals over 6 months). In contrast, group size has no effect on mortality in groups of over 11 animals ($T_{1,51} = -0.44$, $P = 0.66$ for pups; $T_{1,30} = -0.99$, $P = 0.33$ for animals over 6 months). The frequency of subordinate reproduction does not vary with group size and is as high in groups of ≤11 as in groups of >11 (Table 1).
22. T. H. Clutton-Brock *et al.*, *Proc. R. Soc. London Ser. B* **265**, 2291 (1998).
23. In only 51% of litters born to subordinates do individuals survive to emergence, as compared to 85% of litters born to dominants. Most losses occur in the 2 days after birth and are probably caused by infanticide: Mortality is disproportionately high during the 48 hours after birth. In over half of the 10 cases in which females have been seen to kill pups, the killer was the dominant female and was the grandmother of the pups she killed. In all other cases, killers were closely related females, including sisters and aunts of the subordinate female that bred. The probability that subordinate litters will survive to emergence is not significantly related to the mother's age or weight, to the number of helpers present in the group, or to rainfall in the month that the litter was born. After emergence, there is no difference in survival to 3 months between pups born to dominants and subordinates (68.1% ± 8.7 versus 69.8% ± 3.6) [see (24)].
24. Supplementary information is available on *Science* Online at www.sciencemag.org/cgi/content/full/291/5503/478/DC1.
25. We thank the National Parks Board of the Republic of South Africa for permission to work in the Kalahari Gemsbok Park and for their hospitality at Nossob, the staff of the park for their support, and Mr. and Mrs. H Kotze for permission to work on their land at Van Zyl's Rus. The study would not have been possible without the support of members of the Mammal Research Institute, University of Pretoria (including J. Skinner, J. du Toit, and M. Haupt); of the Institute of Cell, Animal and Population Biology, Edinburgh (including J. Pemberton and T. Marshall); and of over 40 assistants, students, postdocs, or visitors who contributed to data collection. For advice, access to data, assistance, or comments we thank S. Doolan, J. Nel, L. Kruuk, J. Barnard, S. White, T. Coulson, T. Jackson, F. Ratnieks, and R. Woodroffe. In planning and carrying through the work, we benefited from the guidance of D. Macdonald and S. Creel. The research is funded by grants from the Natural Environment Research Council and the Biotechnology and Biological Sciences Research Council.

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Variation Among Biomes in Temporal Dynamics of Aboveground Primary Production

Alan K. Knapp and Melinda D. Smith

Interannual variability in aboveground net primary production (ANPP) was assessed with long-term (mean = 12 years) data from 11 Long Term Ecological Research sites across North America. The greatest interannual variability in ANPP occurred in grasslands and old fields, with forests the least variable. At a continental scale, ANPP was strongly correlated with annual precipitation. However, interannual variability in ANPP was not related to variability in precipitation. Instead, maximum variability in ANPP occurred in biomes where high potential growth rates of herbaceous vegetation were combined with moderate variability in precipitation. In the most dynamic biomes, ANPP responded more strongly to wet than to dry years. Recognition of the fourfold range in ANPP dynamics across biomes and of the factors that constrain this variability is critical for detecting the biotic impacts of global change phenomena.

Regional and global patterns in aboveground net primary production (ANPP) and their determinants have long interested ecologists (*1*, *2*). More recently, interest has intensified as projected global changes in climate, nitrogen deposition, and land use (*3*) threaten to alter ecosystem carbon and energy flow. Because alterations in ANPP can influence virtually all ecosystem processes, detecting directional changes in productivity (*4*) against the backdrop of natural variability is important. However, a critical limitation to detecting temporal change is a lack of knowledge of the inherent interannual variability in ANPP in biomes. This variation has been quantified indirectly (*5*), but only now, with the maturation of the Long Term Ecological Research (LTER) network of sites across North America, are long-term data available to assess temporal dynamics in ANPP for a variety of biomes.

Here we present a synthesis of these long-term data to address two questions. First, what are the patterns of interannual variability in ANPP for desert, arctic/alpine, grassland, and forest biomes? Previous estimates of ANPP were unavoidably based on small sample sizes, short time periods, or indirect techniques (*1*, *2*, *6*) with no measure of variability. We summarize ANPP data from 11 sites widely distributed across North America, with an average sampling period of 12 years. These data allow us to calculate more robust ANPP estimates as well as to quantify temporal variability in ANPP across a large productivity gradient.

The second question is, do established climatic predictors of mean ANPP across biomes [precipitation and temperature (*2*)] also

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Division of Biology, Kansas State University, Manhattan, KS 66506, USA.