Current Biology

Extreme and Variable Climatic Conditions Drive the Evolution of Sociality in Australian Rodents

Highlights

- An assessment of whether climatic uncertainty leads to conflict and/or sociality

- Sociality only evolves under harsh environmental conditions

- Reproductive conflict within social groups shapes body size sexual dimorphism

- Mammals may deal with increasing aridity by forming cooperative, social groups

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In Brief

Firman et al. show that sociality evolves under harsh conditions of low rainfall and high temperature variability, never under benign climatic conditions in Australian rodents. They also demonstrate that climate does not directly influence social conflict, but instead shapes competitive phenotypes by favoring the evolution of sociality.

CellPress

Extreme and Variable Climatic Conditions Drive the Evolution of Sociality in Australian Rodents

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SUMMARY

Climate change is generating an intensification of extreme environmental conditions, including frequent and severe droughts [1] that have been associated with increased social conflict in vertebrates [2–4], including humans [5]. Yet, fluctuating climatic conditions have been shown to also promote cooperative behavior and the formation of vertebrate societies over both ecological and evolutionary timescales [6]. Determining when climatic uncertainty breeds social discord or promotes cooperative living (or both) is fundamental to predicting how species will respond to anthropogenic climate change. In light of this, our limited understanding of the order of evolutionary events—that is, whether harsh environments drive the evolution of sociality [6] or, alternatively, whether sociality facilitates the invasion of harsh environments [7]—and of how cooperation and conflict coevolve in response to environmental fluctuation represent critical gaps in knowledge. Here, we perform comparative phylogenetic analyses on Australian rodents (Muridae: Hydromyini) and show that sociality evolves only under harsh conditions of low rainfall and high temperature variability and never under relatively benign conditions. Further, we demonstrate that the requirement to cooperate under harsh climatic conditions generates social competition for reproduction within groups (reflected in the degree of sexual dimorphism in traits associated with intrasexual competition [8]), which in turn shapes the evolution of body size dimorphism. Our findings suggest that as the environment becomes more severe [1], the resilience of some species may hinge on their propensity to live socially, but in so doing, this is likely to affect the evolution of traits that mediate social conflict.

RESULTS AND DISCUSSION

Home to one of the highest levels of diversity of social vertebrates in the world, Australia is a land of environmental extremes and contrasts. This is best exemplified by the difference between the densely forested northern tropic and southern temperate areas, where rainfall is plentiful and predictable (1,000–2,000 mm annually), and the vast central arid zone, where rainfall is low and sporadic (100–400 mm annually) [9], the so-called Australian Outback. Due to high spatial variability in temperature and rainfall, the continent represents a mosaic of climatic regions and environmental niches [10, 11] (Figure 1A). Cyclonic activity in the north leads to highly variable and unpredictable rain falling in the central region, which experiences extended periods of both drought and flooding. The central arid area also tends to have the largest fluctuations in daily temperature, with diurnal temperatures ranging from <10°C to >40°C. Along with geographic isolation, the drying of the land over geological time—in terms of increasing aridity and prevalence of fire—was instrumental in the evolution of Australia's biota [12]. With extant species ranging from relics of the Gondwanan forest to diverse radiations of desert dwellers, it is evident that Australia is rich in biodiversity [12, 13], but how did fluctuating climatic conditions influence Australia's species over evolutionary time?

A major challenge lies in understanding biogeographical processes that have shaped evolution in the absence of primigenial climate data. Comparative analyses that combine molecular phylogenetics with documented life history data have proven to be effective in uncovering patterns of trait emergence and evolution based on changes in environmental conditions [15]. We applied this analytical approach to determine (1) whether harsh and unpredictable environmental conditions promote or impede the formation of societies and (2) how these conditions influence the coevolution of cooperation and conflict in one of Australia's most diverse and widely dispersed mammalian fauna, the hydromyine rodents (Muridae) (Figures 1B, 2A, and 3A–3F; Data S1).

We categorized the social organization of Australian rodents (n = 42) based on published information available in the literature (Table S1). We classified species as social when there was evidence that individuals resided in groups or lived communally in the wild (n = 19). Cooperative behaviors have been documented in most of these species (*sensu* [16]) (e.g., group shelter construction; Figures 3D–3F), which indicates that there is likely to be reproductive competition among females for breeding positions within social groups (e.g., communal nesting) (Table S1). Non-social species were typically categorized from
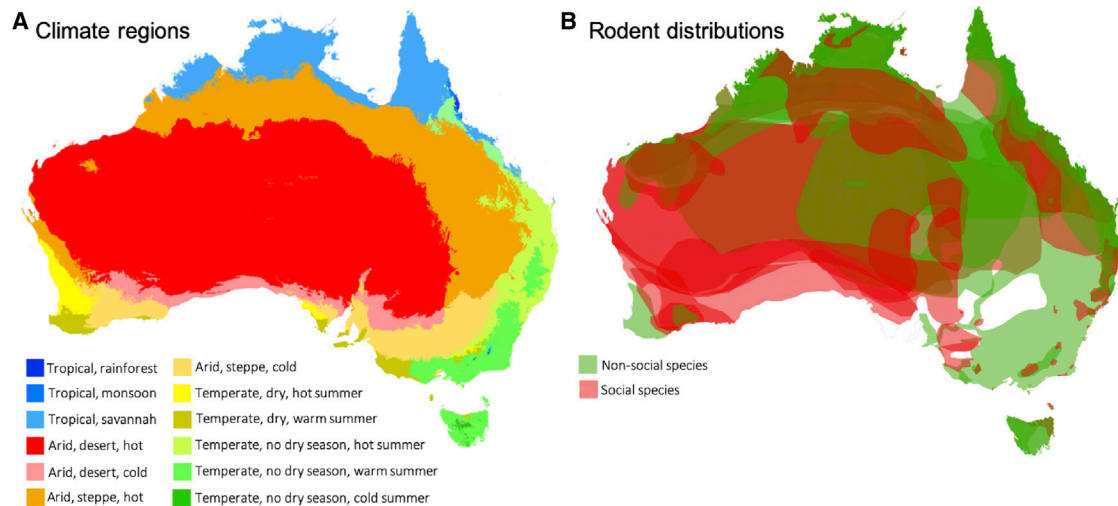
A Climate regions

B Rodent distributions

- Tropical, rainforest
- Tropical, monsoon
- Tropical, savannah
- Arid, desert, hot
- Arid, desert, cold
- Arid, steppe, hot
- Arid, steppe, cold
- Temperate, dry, hot summer
- Temperate, dry, warm summer
- Temperate, no dry season, hot summer
- Temperate, no dry season, warm summer
- Temperate, no dry season, cold summer

- Non-social species
- Social species

Figure 1. Rodents Have Successfully Colonized All of Australia's Climate Regions
(A) Australia's present-day (1980–2016) Köppen-Geiger climate classifications at 1-km resolution [11].
(B) Species distribution polygons used to extract climate data [14]. Polygons are layered by area of occupancy (i.e., largest distribution = bottom layer, smallest distribution = top layer) with 50% transparency.
See Data S1 for each species distribution polygon overlaid on the Köppen-Geiger climate classification map.

reports of individuals demonstrating behaviors that are reflective of a solitary existence (e.g., individually defending a territory from intruding conspecifics; Figures 3A–3C; Table S1) (n = 23). We also generated indices of environmental variation specific to the range of each species by performing a phylogenetic principal-components analysis (PCA) on a series of climatic variables [17] (Figures 1B, 2, and S1A; Tables S2 and S3; Data S1). The first principal component (PC1) was most strongly loaded by low mean rainfall (eigenvector = −0.94) and high temperature variation (eigenvector = 0.93) and therefore provided a measure of environmental extremes, with high PC1 values being indicative of "harsh" conditions and low PC1 values representing "benign" conditions (*sensu* [7, 18]) (Figure 2B; Table S3). We used our indices of environmental variation, sociality status, and the most up-to-date phylogeny (Figure 2A) in a generalized linear model and confirmed that sociality was positively correlated with environmental harshness in this group of mammals (Figure 2C; Table S4). Next, to determine whether harsh and unpredictable environments favor the formation of societies, we assessed specifically whether sociality was a consequence [19] or cause [7] of this relation, which provides evidence of ecological dominance. That is, we tested two competing hypotheses that differ in the direction of causality between sociality and environmental quality: (1) the transition from non-sociality to sociality within harsh environments (social transition hypothesis) [6] and (2) the invasion of harsh environments after sociality has evolved under benign conditions (social conquest hypothesis) [7]. To achieve this, we used our indices of environmental variation and estimated transition rates using a reversible-jump (rj) Markov chain Monte Carlo (MCMC) model [15]. Thus, we estimated whether transitions in sociality were more likely in benign or harsh environments and whether transitions in the type of environment were more likely for social or non-social species. Our analysis provided unequivocal support for the social transition hypothesis, as we found that sociality had evolved only under

harsh conditions of low rainfall and high temperature variability and never under benign conditions (Figure 4).

Further, the magnitude and direction of our estimates of evolutionary transitions align with current knowledge of the ancestry and diversification of the Australian rodents. The initial transition of non-social species from benign to harsh conditions complements the fossil record of Asian ancestry and the colonization of Australia during the early Pliocene, a period of progressing aridity [20, 21] (Figure 4). As Australia's true deserts continued to expand, the arid zone became a hotspot of rodent speciation events before seeding diversity to other climatic regions [22]. In the Pseudomys division of the Australian rodents (i.e., 30 of the 42 species studied here) the most common species transition was from the arid biome to the more temperate biomes [22], which parallels our finding that both forms of social living transitioned secondarily from harsh to benign environments (Figure 4). Thus, it appears that non-social rodent species subjected to harsh conditions tended to either retreat to milder niches or evolve sociality to cope with increasing aridity. The emergence of sociality would be adaptive in the context of facilitating cooperative behaviors that offset the physiological demands of living in a harsh environment (e.g., communal nesting, foraging, constructing shelters, engaging in group territory defense [21, 23–26]; Figures 3D–3F; Table S1). Moreover, cooperating as a group would be an effective strategy for individuals to offset the costs of reproduction [27–29]. An analysis of mammals has linked climatic patterns to the distribution of cooperative breeding on a global scale [30], and many desert rodents, including Australian species, are reported to engage in alloparental care [24, 31]. Consequently, cooperation that facilitates successful reproduction under harsh conditions is likely to be a key factor driving social evolution in rodents and other mammalian taxa (although see [32] on Ctenomyids, in which this does not appear to be the case).
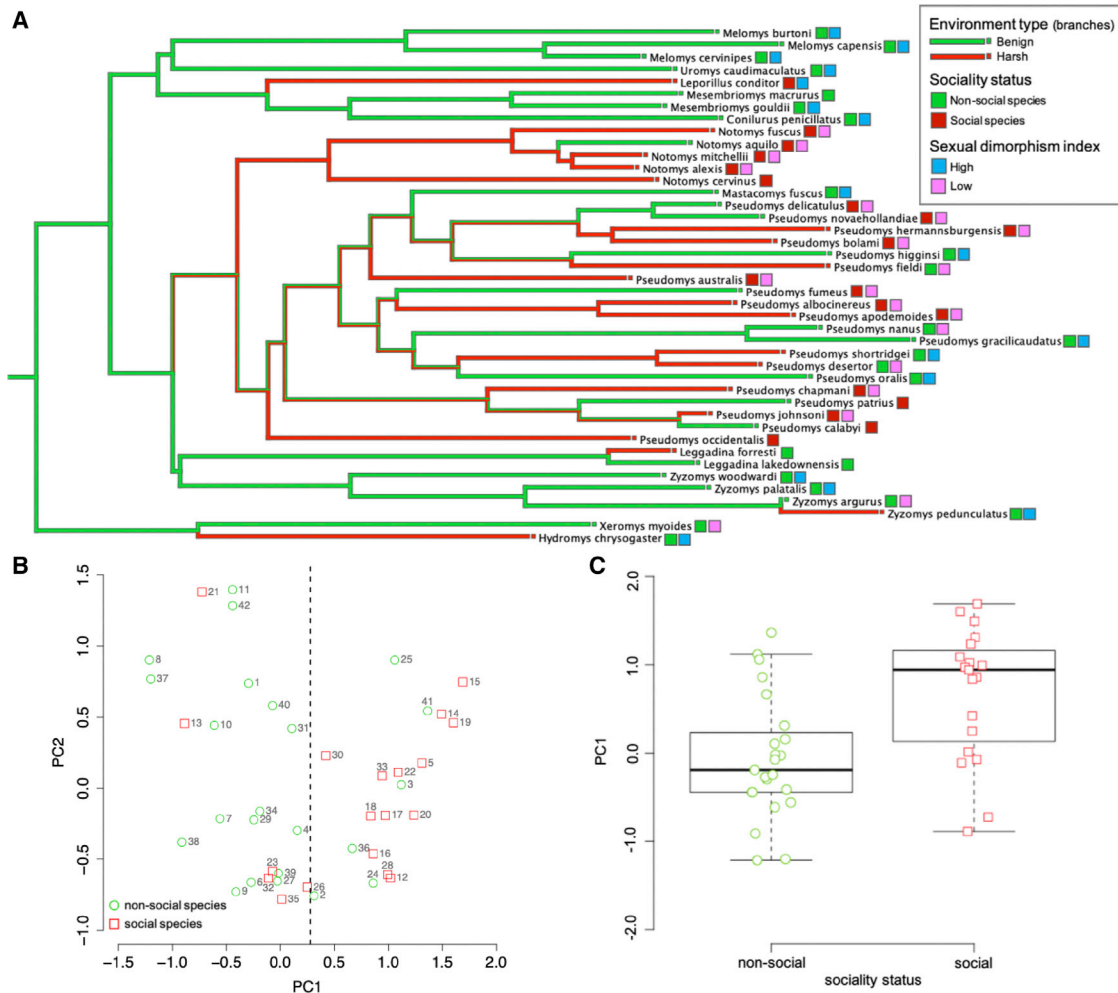
Figure 2. Environment Type, Sociality Status, and Sexual Dimorphism in Australian Hydromyine Rodents

(A) Phylogeny of the Australian rodents used in this study ($n_{species}$ = 42; Methods S1) mapped with environment type (branches), sociality status (boxes), and sexual dimorphism index (boxes). Environment type represents the indices of environmental variation generated by a phylogenetic principal-components analysis (PCA) performed on a series of climatic variables specific to the range of each species (i.e., "harsh" = low rainfall and more variable temperatures, "benign" = high rainfall and less variable temperatures) (Table S3). Sociality status classifications were determined via observations of behavioral traits in published sources (Table S1). The sexual dimorphism index represents the residuals of male body mass regressed on female body mass, as displayed in the inset in Figure 3B ($n_{species}$ = 35). Thus, a "high" index (i.e., values > residual mean) represents a large degree of sexual dimorphism due to relatively large male to female body mass. A "low" index (i.e., values < residual mean) represents a low degree or reversed (i.e., relatively large female to male body mass) sexual dimorphism. We estimate a minimum of 14 transitions in environment type, 5 transitions in sociality status, and 8 transitions in the sexual dimorphism index.

(B) Results of the PCA of climate variables, with species coded by sociality status. Mean PC1 value is displayed (dashed line; left of mean = "benign" environment, right of mean = "harsh" environment). Species are numbered as: (1) *Conilurus penicillatus*, (2) *Hydromys chrysogaster*, (3) *Leggadina forresti*, (4) *Leggadina lakedownensis*, (5) *Leporillus conditor*, (6) *Mastacomys fuscus*, (7) *Melomys burtoni*, (8) *Melomys capensis*, (9) *Melomys cervinipes*, (10) *Mesembriomys gouldii*, (11) *Mesembriomys macrurus*, (12) *Notomys alexis*, (13) *Notomys aquilo*, (14) *Notomys cervinus*, (15) *Notomys fuscus*, (16) *Notomys mitchelli*, (17) *Pseudomys albocinereus*, (18) *Pseudomys apodemoides*, (19) *Pseudomys australis*, (20) *Pseudomys bolami*, (21) *Pseudomys calabyi*, (22) *Pseudomys chapmani*, (23) *Pseudomys delicatulus*, (24) *Pseudomys desertor*, (25) *Pseudomys fieldi*, (26) *Pseudomys fumeus*, (27) *Pseudomys gracilicaudatus*, (28) *Pseudomys hermannsburgensis*, (29) *Pseudomys higginsi*, (30) *Pseudomys johnsoni*, (31) *Pseudomys nanus*, (32) *Pseudomys novaehollandiae*, (33) *Pseudomys occidentalis*, (34) *Pseudomys oralis*, (35) *Pseudomys patrius*, (36) *Pseudomys shortridgei*, (37) *Uromys caudimaculatus*, (38) *Xeromys myoides*, (39) *Zyzomys argurus*, (40) *Zyzomys palatalis*, (41) *Zyzomys pedunculatus*, and (42) *Zyzomys woodwardi*.

(C) Sociality and its association with environment type (PC1). Social species more frequently occur in environments that have lower rainfall and more variable temperatures compared with non-social species, which occur in relatively benign environments (Table S4).

Parallel to climatic conditions favoring the evolution of sociality, environmental uncertainty can also generate conflict that opposes societal formation. Over ecological timescales, for example, environmental uncertainty leads to aggression [5] as well as reproductive conflict [2–4], which can destabilize societies in periods of drought and low resource availability. However, over both ecological (e.g., [27–29, 33, 34]) and evolutionary timescales (e.g., [30, 35]), harsh and fluctuating environments have also been shown to drive the evolution of cooperative behaviors and the formation of societies in birds
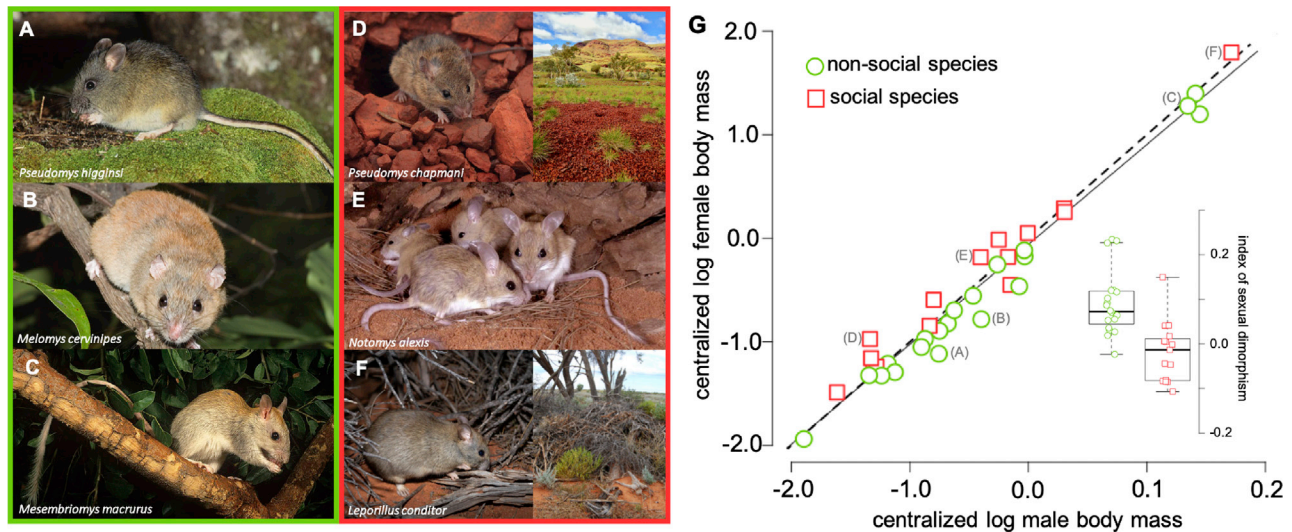
Figure 3. The Australian Hydromyine Rodents Are Morphologically, Ecologically, and Socially Diverse

(A–C) Examples of non-social species (green panel; Table S1). (A) Female long-tailed mice occupy exclusive home ranges, while male home ranges overlap to some degree. The range of the long-tailed mouse is restricted to the temperate region of Tasmania (credit: Jiri Lochman). (B) Fawn-footed melomys, which occupy Queensland's rainforests and wet sclerophyll forests, live solitarily and hold exclusive home ranges that they defend against intruders (credit: Narelle Power). (C) Golden-backed tree rats live a solitary existence in the northern tropical savanna woodlands (credit: Jiri Lochman).

(D–F) Examples of social species (red panel; Table S1). (D) Western pebble-mound mice, which occupy Western Australia's semi-arid Pilbara region, work cooperatively in groups to build pebble mounds above their burrows (credits: A. Gibson-Vega and R. Firman). (E) Spinifex hopping mice are distributed across the arid region, where they dig out complex tunnel systems with multiple nest chambers (credit: Steve Parish). (F) Greater stick-nest rats live communally in wooden nests, some of which are believed to have lasted >10,000 years. Once occurring over most of semi-arid South Australia, there is now only one naturally occurring population on Franklin Island in the Great Australian Bight (credits: Australian Wildlife Conservancy, Arid Recovery).

(G) The relation between male and female body mass demonstrates that selection acts differently on the sexes in social (n = 19) and non-social (n = 23) Australian rodents (Tables S2 and S4). Since mean body mass and sociality status were significantly correlated, we plotted the centralized values of body mass in a comparable way between social and non-social species (i.e., we subtracted the mean body mass in each status from male and female body masses for each species).

The species pictured in (A)–(F) are indicated. The inset shows the index of sexual dimorphism (i.e., the residuals of male body mass regressed on female body mass). Lines of the fit of allometry (solid) and perfect isometry (dashed) are displayed.

and mammals. It remains to be tested whether environmental uncertainty generates social conflict on an evolutionary timescale and whether and how cooperation and conflict coevolve at this scale.

Social conflict in the form of intrasexual competition over reproductive opportunities occurs in most animals, where male-male competition over resources and mates typically selects for males to be larger, more aggressive, and better armed than females [36]. However, in social species, it is both males and females that are limited by reproductive opportunity, and therefore it is individuals of both sexes that are subjected to intense conflict as they strive to acquire a dominant reproductive position within the group [37]. Thus, the strength of selection acting on traits used in competition for access to mates (intrasexual selection) or other resources linked to reproduction (social selection) is expected to be equivalent for both males and females [8, 38]. To this end, the degree of sexual dimorphism may be representative of the direction and level of intrasexual conflict, for example, with intense female conflict in social species leading to reduced or reversed sexual dimorphism relative to non-social species [8, 37]. Examples include intersexual differences in plumage and body size from selection favoring the evolution of traits that increase female attractiveness, as well as their reproductive opportunity, in African starlings [8].

Increased body size for exerting dominance and mitigating conflict will be especially important for females of social species that lack elaborate displays or ornaments used in mate attraction, as seen in many mammals (e.g., see [38]), including most rodents. When there are limited breeding positions within social groups—whether cooperative breeders or not—dominant females may forcibly disrupt the reproductive physiology of subordinate females by subjecting them to chronic physiological stress through targeted aggression [4, 39]. In such cases, female body size is expected to be linked to competitive ability and play a key role in facilitating reproductive opportunity.

To test the idea that in addition to promoting sociality, harsh and unpredictable climatic conditions generate social conflict in Australian rodents (n = 35) and have led to the evolution of traits that likely mediate this conflict, we applied a phylogenetic generalized linear model to the residuals of the body size allometry between the sexes (i.e., the degree of sexual dimorphism) (Table S4). Our analysis returned no evidence that climate directly influenced sexual dimorphism, but it did reveal patterns of male-biased sexual dimorphism in non-social species and reduced sexual dimorphism in social species (Figure 3G; Table S4). The observed patterns of sexual dimorphism in social versus non-social rodents could be due to intersexual differences in reproductive requirements and attributable to the fact
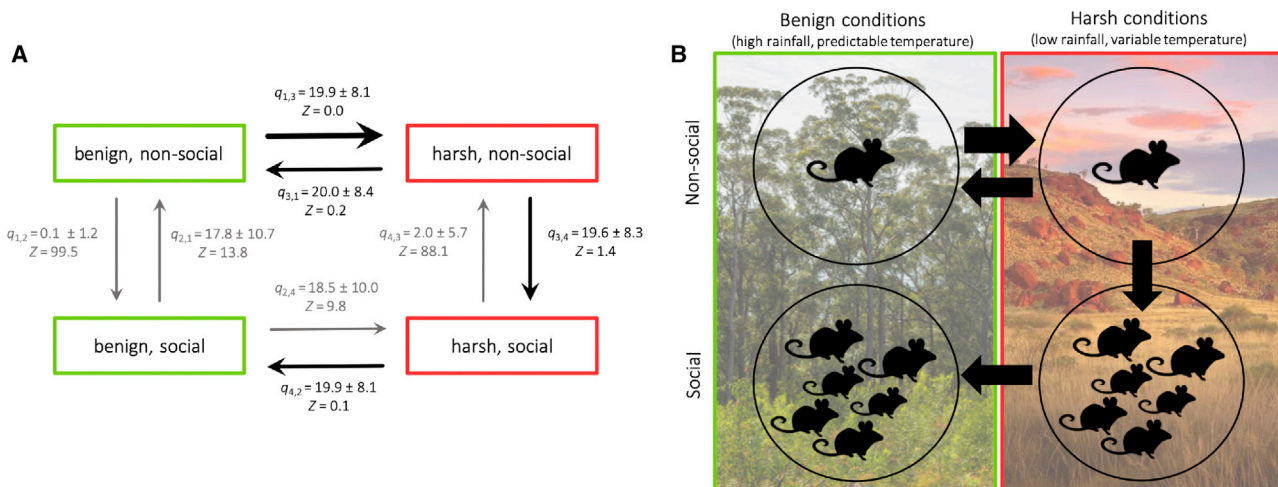
Figure 4. Harsh Environments Drive the Evolution of Sociality

(A) Evolutionary transition rates between sociality status (Table S1) and type of environment (Table S2), where Z = percentage of times the transitions between two states were assigned to zero in the rj MCMC chain and q = mean (±SD) of the posterior probabilities for the transition rates estimated by our dependent model of sociality status and environment type evolution. Arrow thickness and color represent the magnitude of the transition (q), where gray is improbable and black is probable.

(B) Summary graphic of the probable transitions. Sociality evolves under harsh conditions, but never under benign conditions. Once sociality is gained, it is never lost, and social species transition only from harsh to benign environments. Sensitivity analyses, which varied the environment type for a subset of species, produced results that were qualitatively similar to what is displayed here (see Figure S2).

that females need to maintain a minimum body size even under harsh conditions (i.e., for gestation and lactation). Certainly, low resource availability coupled with the physiological limits of small-bodied mammals are likely to favor a general reduction in body size [40]. However, a phylogenetic generalized linear model testing the relation between PC1 and mean body mass suggested that this is not the case for Australian rodents (Table S4). Furthermore, phylogenetic path analysis confirmed that sociality is a stronger driver of sexual dimorphism than is environmental harshness (Figure S1B; Table S5). It appears, therefore, that in social rodents, there is comparable reproductive skew in both sexes, and success in intrasexual competition is equally important in males and females. Variation in sexual dimorphism may be driven by relaxed selection on male body size in social species relative to non-social species, for example, due to differences in paternal care in which, in social groups, males invest in rearing offspring instead of competing for additional mating opportunities [41]. However, this explanation is incompatible with evidence suggesting that paternal care is favored when paternity is certain [42]. Indeed, one major cost of group living for males is often the inability to prevent females from mating multiply [43]. Therefore, the pattern observed here is most likely the consequence of increased selection on female body size in social groups in which competition for limited reproductive opportunity is intense.

In summary, our comparative analyses have shown that extreme and uncertain climates favor cooperative strategies and underlies the evolution of complex societies, which in turn generate social competition for reproductive opportunities and shapes the phenotypic evolution of traits used to mediate intrasexual conflict. In other words, harsh climatic conditions of low rainfall and high temperature variation shape both cooperative (directly) and competitive (indirectly) strategies in Australian rodents by favoring the evolution

of sociality. The potential for ecologically significant evolutionary change, which is widely documented in nature and can occur over tens of generations or fewer, indicates that our findings are pertinent to understanding organismal adaptation in this era of accelerating environmental uncertainty [44]. Although many animals are predicted to be able to track their preferred climatic niches and shift their geographic range as conditions change [45], some models hypothesize that the dispersal capacities of most species will eventually be outpaced by climate change [46]. In these cases, a change in behavior may be an effective response to altered climatic and ecological conditions in the short term through phenotypic plasticity and later via evolutionary adaptation [47]. We have shown that sociality has played a key role in the adaptation of Australian rodents to climatic heterogeneity. Specifically, our results support a long-standing theory that sociality evolves under the selective pressure of severe ecological constraints [23]. Although we found no direct evidence that climate uncertainty over evolutionary timescales generates social conflict by looking at evolved patterns of sexual dimorphism, our investigation does suggest that intrasexual conflict over reproduction simultaneously intensifies as cooperation is favored under harsh conditions, which leads to trait evolution. As Australia's climate becomes drier under contemporary climate change [11], we may observe that social evolution further facilitates the continental diversification of these rodent species. Moreover, with a projected 10% expansion of global drylands over the next 80 years [1], sociality may emerge as a survival strategy for mammals worldwide, but in turn, this could also affect the evolution of traits that mediate conflict.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at https://doi.org/10.1016/j.cub.2019.12.012.

AUTHOR CONTRIBUTIONS

Conceptualization, R.C.F. and D.R.R.; Investigation, R.C.F. and J.M.M.; Resources, K.C.R. (phylogeny); Formal Analysis, B.A.B.; Visualization, B.A.B., R.C.F., D.R.R., and J.M.M.; Writing – Original Draft, R.C.F., D.R.R., and B.A.B.; Writing – Review & Editing, R.C.F., B.A.B., D.R.R., J.M.M., and K.C.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Feng, S., and Fu, Q. (2013). Expansion of global drylands under a warming climate. Atmos. Chem. Phys. *13*, 10081–10094.

2. Nichols, H.J., Bell, M.B.V., Hodge, S.J., and Cant, M.A. (2012). Resource limitation moderates the adaptive suppression of subordinate breeding in a cooperatively breeding mongoose. Behav. Ecol. *23*, 635–642.

3. Leighton, G.M., and Vander Meiden, L.N. (2016). Sociable weavers increase cooperative nest construction after suffering aggression. PLoS One *11*, e0150953.

4. Cant, M.A., Nichols, H.J., Johnstone, R.A., and Hodge, S.J. (2014). Policing of reproduction by hidden threats in a cooperative mammal. Proc. Natl. Acad. Sci. USA *111*, 326–330.

5. Shaffer, L.J. (2017). An anthropological perspective on the climate change and violence relationship. Curr. Clim. Change Rep. *3*, 222–232.

6. Shen, S.-F., Emlen, S.T., Koenig, W.D., and Rubenstein, D.R. (2017). The ecology of cooperative breeding behaviour. Ecol. Lett. *20*, 708–720.

7. Cornwallis, C.K., Botero, C.A., Rubenstein, D.R., Downing, P.A., West, S.A., and Griffin, A.S. (2017). Cooperation facilitates the colonization of harsh environments. Nat. Ecol. Evol. *1*, 57.

8. Rubenstein, D.R., and Lovette, I.J. (2009). Reproductive skew and selection on female ornamentation in social species. Nature *462*, 786–789.

9. Australian Bureau of Meteorology (2018). Average annual, seasonal and monthly rainfall (Australian Bureau of Meteorology). http://www.bom.gov.au.

10. CSIRO; Australian Bureau of Meteorology (2018). State of the Climate 2018. http://www.bom.gov.au/state-of-the-climate/.

11. Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., and Wood, E.F. (2018). Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci. Data *5*, 180214.

12. Joseph, L., Yeates, D.K., Miller, J., Spratt, D., Gledhill, D., and Butler, A. (2014). Australia's biodiversity: major features. In Biodiversity: Science and Solutions for Australia, S. Morton, A. Sheppard, and M. Lonsdale, eds. (CSIRO Publishing), pp. 13–36.

13. Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A.J., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., et al. (2008). Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. Mol. Ecol. *17*, 4398–4417.

14. IUCN (2016). IUCN Red List of Threatened Species. Version 2016.1. htttp://www.iucnredlist.org.

15. Pagel, M., and Meade, A. (2006). Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. Am. Nat. *167*, 808–825.

16. Rubenstein, D.R., and Abbott, P. (2018). The evolution of social evolution. In Comparative Social Evolution, D.R. Rubenstein, and P. Abbott, eds. (Cambridge University Press), pp. 1–18.

17. Kozak, K.H., Graham, C.H., and Wiens, J.J. (2008). Integrating GIS-based environmental data into evolutionary biology. Trends Ecol. Evol. *23*, 141–148.

18. Botero, C.A., Dor, R., McCain, C.M., and Safran, R.J. (2014). Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. Mol. Ecol. *23*, 259–268.

19. Brooks, K.C., Maia, R., Duffy, J.E., Hultgren, K.M., and Rubenstein, D.R. (2017). Ecological generalism facilitates the evolution of sociality in snapping shrimps. Ecol. Lett. *20*, 1516–1525.

20. Rowe, K.C., Reno, M.L., Richmond, D.M., Adkins, R.M., and Steppan, S.J. (2008). Pliocene colonization and adaptive radiations in Australia and New Guinea (Sahul): multilocus systematics of the old endemic rodents (Muroidea: Murinae). Mol. Phylogenet. Evol. *47*, 84–101.

21. Breed, B., and Ford, F. (2007). Native Mice and Rats (CSIRO Publishing).

22. Smissen, P.J., and Rowe, K.C. (2018). Repeated biome transitions in the evolution of Australian rodents. Mol. Phylogenet. Evol. *128*, 182–191.

23. Emlen, S.T. (1982). The evolution of helping. I. An ecological constraints model. Am. Nat. *119*, 29–39.

24. Faulkes, C.G., Bennett, N.C., Bruford, M.W., O'Brien, H.P., Aguilar, G.H., and Jarvis, J.U.M. (1997). Ecological constraints drive social evolution in the African mole-rats. Proc. Biol. Sci. *264*, 1619–1627.

25. Ebensperger, L.A., and Bozinovic, F. (2000). Communal burrowing in the hystricognath rodent, *Octodon degus*: a benefit of sociality? Behav. Ecol. Sociobiol. *47*, 365–369.

26. Ritchie, M.E., and Belovsky, G.E. (1990). Sociality of Columbian ground squirrels in relation to their seasonal energy intake. Oecologia *83*, 495–503.

27. Guindre-Parker, S., and Rubenstein, D.R. (2018). Multiple benefits of alloparental care in a fluctuating environment. R. Soc. Open Sci. *5*, 172406.

28. Guindre-Parker, S., and Rubenstein, D.R. (2018). No short-term physiological costs of offspring care in a cooperatively breeding bird. J. Exp. Biol. *221*, jeb186569.

29. Blumstein, D.T., and Armitage, K.B. (1999). Cooperative breeding in marmots. Oikos *84*, 369–382.

30. Lukas, D., and Clutton-Brock, T. (2017). Climate and the distribution of cooperative breeding in mammals. R. Soc. Open Sci. *4*, 160897.

31. Happold, M. (1976). Social behavior of the conilurine rodents (Muridae) of Australia. Z. Tierpsychol. *40*, 113–182.

32. Lacey, E.A., and Wieczorek, J.R. (2003). Ecology of sociality in rodents: a Ctenomyid perspective. J. Mammal. *84*, 1198–1211.

33. Covas, R., du Plessis, M.A., and Doutrelant, C. (2008). Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. Behav. Ecol. Sociobiol. *63*, 103–112.

34. Canário, F., Matos, S., and Soler, M. (2004). Environmental constraints and cooperative breeding in the Azure-Winged Magpie. Condor *106*, 608–617.

35. Rubenstein, D.R., and Lovette, I.J. (2007). Temporal environmental variability drives the evolution of cooperative breeding in birds. Curr. Biol. *17*, 1414–1419.

36. Andersson, M. (1994). Sexual Selection (Princeton University Press).

37. West-Eberhard, M.J. (1983). Sexual selection, social competition, and speciation. Q. Rev. Biol. *58*, 155–183.

38. Clutton-Brock, T.H., Hodge, S.J., Spong, G., Russell, A.F., Jordan, N.R., Bennett, N.C., Sharpe, L.L., and Manser, M.B. (2006). Intrasexual competition and sexual selection in cooperative mammals. Nature *444*, 1065–1068.

39. Clutton-Brock, T.H., and Huchard, E. (2013). Social competition and selection in males and females. Philos. Trans. R. Soc. Lond. B Biol. Sci. *368*, 20130074.

40. Alhajeri, B.H., and Steppan, S.J. (2016). Association between climate and body size in rodents: a phylogenetic test of Bergmann's rule. Mamm. Biol. *81*, 219–225.

41. Magrath, M.J.L., and Komdeur, J. (2003). Is male care compromised by additional mating opportunity? Trends Ecol. Evol. *18*, 424–430.

42. Lukas, D., and Clutton-Brock, T.H. (2013). The evolution of social monogamy in mammals. Science *341*, 526–530.

43. Lambert, C.T., Sabol, A.C., and Solomon, N.G. (2018). Genetic monogamy in socially monogamous mammals is primarily predicted by multiple life history factors: a meta-analysis. Front. Ecol. Evol. *6*, 139.

44. Carroll, S.P., Hendry, A.P., Reznick, D.N., and Fox, C.W. (2007). Evolution on ecological time-scales. Funct. Ecol. *21*, 387–393.

45. Diamond, S.E. (2018). Contemporary climate-driven range shifts: putting evolution back on the table. Funct. Ecol. *32*, 1652–1665.

46. Schloss, C.A., Nuñez, T.A., and Lawler, J.J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proc. Natl. Acad. Sci. USA *109*, 8606–8611.

47. Wong, B.B.M., and Candolin, U. (2015). Behavioral responses to changing environments. Behav. Ecol. *26*, 665–673.

48. Bond, N.R. (2015). hydrostats: hydrologic indices for daily time series data. R package version 0.2.4 (R Foundation for Statistical Computing).

49. Revell, L.J. (2011). phytools: An R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. *3*, 217–223.

50. R Core Team (2018). R: A language and environment for statistical computing (R Foundation for Statistical Computing).

51. van der Bijl, W. (2018). *phylopath*: easy phylogenetic path analysis in R. PeerJ *6*, e4718.

52. Maddison, W.P., and Maddison, D.R. (2011). Mesquite: a modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org.

53. ESRI (2010). ArcGIS Version 10.0 (Environmental Systems Research Institute).

54. Stamatakis, A. (2006). RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics *22*, 2688–2690.

55. Stamatakis, A., Hoover, P., and Rougemont, J. (2008). A rapid bootstrap algorithm for the RAxML Web servers. Syst. Biol. *57*, 758–771.

56. Miller, M.A., Pfeiffer, W., and Schwartz, T. (2010). Creating the CIPRES Science Gateway for inference of large phylogenetic trees. https://ieeexplore.ieee.org/document/5676129.

57. Colwell, R.K. (1974). Predicability, constancy, and contingency of periodic phenomena. Ecology *55*, 1148–1153.

58. Fairbarn, D.J. (1997). Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annu. Rev. Ecol. Syst. *28*, 659–687.

59. Gonzalez-Voyer, A., and von Hardenberg, A. (2014). An introduction to phylogenetic path analysis. In Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology, L.Z. Garamszegi, ed. (Springer), pp. 201–229.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Methods S1	Kevin Rowe (Museum Victoria)	N/A
Software and Algorithms		
hydrostats	[48]	https://cran.r-project.org/web/packages/hydrostats/index.html
phytools	[49]	https://cran.r-project.org/web/packages/phylotools/index.html
R	[50]	https://www.r-project.org
phylopath	[51]	https://cran.r-project.org/web/packages/phylopath/index.html
Mesquite	[52]	http://mesquiteproject.org

LEAD CONTACT AND MATERIALS AVAILABILITY

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Renée Firman (renee.firman@uwa.edu.au). This study did not generate new or unique materials.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

No new populations or experimental subjects were included in this work. Sociality status, body mass, and litter size data for the rodent species studied were obtained from the literature as described in the section "Data Collection" below.

METHOD DETAILS

Data collection

We used Australia's mosaic of climatic regions and environmental niches to investigate whether climate variation shapes social living (a proxy for cooperation) and/or social competition for reproduction (a proxy for conflict). We collected sociality status, body mass, and litter size data for the hydromyine rodent species of Australia from the literature. For those species included in our phylogeny, and for which there was available data, we categorized each as either social ($n_{species}$ = 19) or non-social ($n_{species}$ = 23) (Table S1). Thus, we screened the primary literature and classified species based on reports of behavioral trait(s) or observation(s) related to social behavior (Table S1). We classified species as social when there was evidence that individuals resided in groups or lived communally in the wild. Our definition of "social" included elements of cooperation (*sensu* [16]) for many of these species (e.g., communal nesting, group shelter construction; Figures 3D–3F; Table S1). Non-social species were typically categorized from reports of individuals demonstrating behaviors reflective of a solitary existence (e.g., individually defending a territory from intruding conspecifics) (Table S1).

In social species, selection acts with comparable intensity on traits used in intrasexual competition in both males and females [8, 38]. The degree of sexual dimorphism in these traits is often reduced, and therefore can be used as an indication of the magnitude of social conflict within that species. To this end, we collected male and female body mass data from published and unpublished sources ($n_{species}$ = 35; Table S2). For 32 species, we calculated mean male and female body mass taken from multiple sources and used these values in our analyses. For three species, mean body mass data were sourced from a single reference. We excluded body mass data measured from individuals that had been maintained in captivity. Mean litter size data, which was included as a covariate in our analysis of sexual dimorphism, was primarily obtained from a single source (Table S2).

Climatic data

We generated climatic data for the 42 Australian hydromyine rodent species that we had classified as either social or non-social (Table S2). Polygons representing the extant ranges (as of July 2017) of Australian rodent species that were included in our phylogeny were obtained from the IUCN Red List database (Figure 1B; Data S1) [14]. Areas of distribution were calculated by transforming the IUCN species distribution polygons to the Australia Albers Equal Area (1994 Geocentric Datum of Australia) projection system (Data S1). Where species distributions spanned different countries (i.e., for *Conilurus penicillatus*, *Hydromys chrysogaster*, *Melomys burtoni*, *Pseudomys delicatulus*, *Uromys caudimaculatus* and *Xeromys myoides*) polygons of their Australian range were extracted

from the larger geographic dataset using the "clip" tool in ArcGIS 10.1 [53]. The Australian range of each species was represented by single or multiple polygons depending on the species' distribution range. Where polygons for a single species overlapped or were segmented based on state or territory borders, the polygons were merged using the "dissolve" tool in ArcGIS 10.1 [53] to obtain a single polygon representing the full distribution range of a given species. ASCII files of gridded high-resolution (5 km × 5 km) climate data were obtained from the Australian Bureau of Meteorology and converted to raster grids in ArcGIS. We ran a "zonal statistics" analysis using the Spatial Analyst extension of ArcGIS for the climate data for each species extant Australian distribution, and calculated the total (sum) rainfall and mean daily maximum temperature for each week from 1900 until 2017 for each species distribution.

Phylogeny

We estimated phylogenetic relationships among 46 species of murine rodents, including 42 species of Australian hydromyine rodents and four outgroup species (Methods S1). For each of these species we compiled available DNA sequences from five commonly sequenced genes, including a mitochondrial protein coding locus (cytochrome b) and 4 nuclear exons (exon 11 of BRCA1, exon 10 of GHR, exon 1 of IRBP, and the single exon of RAG1). These data were drawn largely from the alignments of Smissen and Rowe [22], but included four additional species for this study. We estimated phylogenetic relationships using maximum likelihood in RAxML via the CIPRES Science Gateway [54–56]. Substitution models, partitions and other parameters followed Smissen and Rowe [22].

QUANTIFICATION AND STATISTICAL ANALYSIS

Characterizing environmental conditions

We calculated the mean, variance, and predictability of rainfall and mean daily maximum temperature for each species' distribution prior to analyses. Among-year weekly predictability was determined via Colwell's P (using a modified version of '*Colwells*' function in R package 'hydrostats'), an index that captures variation in onset, intensity, and duration of periodic phenomena ranging from 0 (completely unpredictable) to 1 (completely predictable) [57, 48]. We generated an index of environmental quality using a phylogenetic principle components analysis (PCA) from the mean, variance and Colwell's P of rainfall and temperature for each species' distribution (Tables S2 and S3). The PCA produced two principal components (PC1, PC2) that collectively accounted for 73% of the variation. Traits that contributed most to these components included mean rainfall and temperature variation for PC1, and Colwell's P of both rainfall and temperature for PC2 (Table S3). PC1 was loaded by (i) low mean rainfall (eigenvector = −0.94) and (ii) high temperature variation (eigenvector = 0.93). Therefore, high PC1 values were indicative of "harsh" conditions and low PC1 values represented "benign" conditions (*sensu* [7, 18]) (Figure 2B; Table S3).

Evolutionary transition rates between sociality status and environment type

We tested for correlated evolution between sociality and environmental conditions (PC1, PC2) in the Australian rodents using reversible-jump (rj) MCMC implemented in the software *BayesTraits* [15] *V3*. This approach also enabled us to infer whether transitions in type of environment depended on the sociality status, or whether transitions in sociality status depended on the type of environment. Since discrete classifications of environmental types is required for the rj MCMC analysis to infer the order of evolutionary transitions, we transformed PC1 and PC2 into binary classifications. We coded values below and above the mean PC value as 0 and 1, respectively, which maintained comparable sample sizes in the binary datasets (PC1: [0; wet and constant temperature; "benign"] = 23, dry [1; dry and variable temperature; "harsh"] = 19; PC2: [0; predictable temperature] = 22, [1; unpredictable temperature] = 20; Figures 2B and S1A). Each species could then be allocated to one of four categories described as [environment type, sociality status], such that category 1 = [0, 0], 2 = [0, 1], 3 = [1, 0], and 4 = [1, 1].

We then inferred the ancestral state of this combination of traits through a likelihood reconstruction method [15] in a Markov, k-status, one-parameter model with four states, using the tool "trace character history" in Mesquite v3.6 [52]. The ancestral state was more likely to be a benign environment (PC1 lower than mean) and lack of sociality (proportional likelihood = 0.844), whereas any other combination of PC1 and sociality was considerably less likely (proportional likelihoods between 0.025 and 0.065). This is consistent with current knowledge about the ancestors of the Australian rodents, which arrived from Asia during a time when the continent was becoming progressively drier but before true deserts had formed (i.e., the late Miocene; < 6.5 Mya) [20, 21].

Next, we used the program DISCRETE in *BayesTraits*, which allows all possible forward and reverse transitions between the states of each category, but in a 'dependent' model that assumes that transitions involving simultaneous change in both sociality status and environment type do not occur, and hence generating eight possible transitions (Figure 4A). We ran a rj MCMC chain for 5,050,000 iterations, with a burn-in period of 50,000 iterations, after which the chain was sampled every 1,000th iteration. We specified exponential priors seeded from a hyperprior with a uniform distribution on the interval of 0–100. We ran the rj MCMC chains with (i) a dependent model, where transitions in sociality status depended on the environment type and vice versa, and (ii) an independent model, where transitions on these traits were mutually independent of each other. We compared these models on the basis of Bayes factors (BFs), which are two times the difference in the marginal likelihoods of the best-fit and worse-fit models. These marginal likelihoods were estimated with the stepping stone sampler implemented in the "stones" command in BayesTraits, setting the sampler to use 100 stones and run each stone for 10,000 iterations.

Our separate analyses using PC1 and PC2 generated BFs of 6.04 and 0.14, respectively. Typically, a BF < 2 is considered to provide weak evidence of correlated evolution, while a BF > 5 is considered to provide strong evidence for this evolutionary model [15].

Therefore, in the main text we only discuss the results of the evolutionary transitions between PC1 and sociality status. We further explored the dependent model involving PC1, examining the posterior distributions of the transition parameters (named q_{ij}, for transitions from category i to category j), extracting their mean and standard deviation, and quantifying the frequency with which each of them was assigned to zero (Z) in the dependent model rj MCMC chain. We considered transitions to be probable events when $Z < 5\%$, and improbable events otherwise. We examined the sensitivity of our results to subjective threshold boundaries (i.e., 45th/55th and 60th/40th), which produced results that were qualitatively similar to those from using the mean (Figure S2). We present only the results from using the mean because it (i) represents an objective parameter, and (ii) provides a balanced binary split of the dataset.

Comparative analyses of sexual dimorphism evolution

We investigated the evolution of sexual dimorphism in relation to environment condition using the binary versions of PC1 and PC2 values used in the analyses of correlated evolution described above. We first regressed female body mass onto male body mass (both natural logarithm transformed) for the 35 rodent species for which we had body mass data. We used the residuals from this regression as an index of sexual dimorphism—positive residuals represent species where females are heavier than males and negative residuals represent species where males are heavier than females. We then tested whether the environment condition influenced the degree of sexual dimorphism using a phylogenetic generalized linear model fit with the package *phytools* [49] in R version 3.5.0 [50]. In this model, we also included: sociality status, litter size; and mean body mass (in order to discount the potential effect of Rensch's rule [58]) (Table S4). We also ran this analysis using the differences of body sizes (i.e., female body mass minus male body mass) instead of the residuals, which returned the same result (analysis not shown). The phenotypic expression of traits will ultimately be a synthesis of the many complex selective processes that harsh environments impose [40]. We therefore looked for evidence that low-rainfall conditions had influenced the evolution of body size, generally, in our study system. A phylogenetic generalized linear model revealed that there was no relationship between PC1 (low rainfall, variable temperatures) and mean body size in the Australian rodents (Table S4).

Disentangling the effects of environment and sociality on sexual dimorphism

We investigated the causal relationships between environmental type, sociality status (social or non-social) and sexual dimorphism using a phylogenetic path analysis [59] (Figure S1B; Table S5). Here, we used the PC1 score from our phylogenetic PCA on climatic parameters as our proxy for environmental type (described above), and the residuals from the regression of female body mass on male body mass as our index for sexual dimorphism (described above in the sexual dimorphism analysis). We considered three possible models (represented by the directed acyclic graphs in Figure S1B) where: (1) environment type influenced sexual dimorphism indirectly via its effect on sociality status; (2) environment type independently influenced sexual dimorphism and sociality status; and (3) both environment type and sociality status independently influenced sexual dimorphism. The directionality of the effects in these models were based on our results of the transition analyses described earlier, and also on our decision to always include sexual dimorphism as a dependent variable. Models were used in a model averaging approach using the function *average* in the R package *phylopath* [51], using the 'full' method.

DATA AND CODE AVAILABILITY

The dataset used in this study is provided as supplementary material (Tables S1 and S2). We will provide our R-code upon request.