

8. Bacastow, R. The effect of temperature change of the warm surface waters of the oceans on atmospheric CO₂. *Glob. Biogeochem. Cycles* **10**, 319–333 (1996).

9. Cane, M. & Clement, A. *Mechanisms of Global Climate Change at Millennial Time Scales* AGU Geophysical Monograph 112 (eds Clark, P., Webb, R. & Keigwin, L.) 373–383 (American Geophysical Union, Washington DC, 1999).

10. Broecker, W. & Henderson, G. The sequence of events surrounding Termination II and their implications for the cause of glacial-interglacial CO₂ changes. *Paleoceanography* **13**, 352–364 (1998).

11. Shackleton, N. The 100,000-year ice age cycle identified and found to lag temperature, carbon dioxide, and orbital eccentricity. *Science* **289**, 1897–1902 (2000).

12. Steig, E. *et al.* Synchronous climate changes in Antarctica and the North Atlantic. *Science* **282**, 92–95 (1998).

13. Lea, D., Mashiotta, T. & Spero, H. Controls on magnesium and strontium uptake in planktonic foraminifer determined by live culture. *Geochim. Cosmochim. Acta* **63**, 2369–2379 (1999).

14. Elderfield, H. & Ganssen, G. Past temperature and δ¹⁸O of surface ocean waters inferred from foraminiferal Mg/Ca ratios. *Nature* **405**, 442–445 (2000).

15. Hastings, D., Kienast, M., Steinke, S. & Whitko, A. A Comparison of three independent paleotemperature estimates from a high resolution record of deglacial SST records in the tropical South China Sea. *Eos* **82**, PP12B-10 (2001).

16. Rosenthal, Y., Lohmann, G., Lohmann, K. & Sherrell, R. Incorporation and preservation of Mg in *Globigerinoides sacculifer*: Implications for reconstructing the temperature and ¹⁸O/¹⁶O of seawater. *Paleoceanography* **15**, 135–145 (2000).

17. Farrell, J. & Prell, W. Climatic change and CaCO₃ preservation: An 800,000 year bathymetric reconstruction from the central equatorial Pacific Ocean. *Paleoceanography* **4**, 447–466 (1989).

18. Martinson, D. *et al.* Age dating and the orbital theory of the ice-ages: development of a high-resolution 0–300,000 year chronostratigraphy. *Quat. Res.* **27**, 1–29 (1987).

19. Schrag, D., Hampt, G. & Murray, D. Pore fluid constraints on the temperature and oxygen isotopic composition of the glacial ocean. *Science* **272**, 1930–1932 (1996).

20. Epstein, S., Buchsbaum, R., Lowenstam, H. & Urey, H. Revised carbonate-water isotopic temperature scale. *Geol. Soc. Am. Bull.* **64**, 1315–1325 (1953).

21. Broecker, W. Mountain glaciers: Recorders of atmospheric water vapor content. *Glob. Biogeochem. Cycles* **11**, 589–597 (1997).

22. Petit, J. *et al.* Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* **399**, 429–436 (1999).

23. Hastenrath, S. On meridional heat transports in the world ocean. *J. Phys. Ocean.* **12**, 922–927 (1982).

24. White, W. B. & Peterson, R. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature* **380**, 699–702 (1996).

25. Koutavas, A., Lybch-Stieglitz, J., Marchitto, T. M. & Sachs, J. El Niño-like pattern in ice age tropical Pacific sea surface temperature. *Science* **297**, 226–230 (2002).

26. Stott, L., Poulsen, C., Lund, S. & Thunell, R. Super ENSO and global climate oscillations at millennial time scales. *Science* **297**, 222–226 (2002).

27. Boyle, E., Labeyrie, L. & Duplessy, J.-C. Calcitic foraminiferal data confirmed by cadmium in aragonitic *Hoeglundina*; application to the last glacial maximum in the northern Indian Ocean. *Paleoceanography* **10**, 881–900 (1995).

28. Dekens, P. S., Lea, D., Pak, D. & Spero, H. Core top calibration of Mg/Ca in tropical foraminifer: Refining paleotemperature estimation. *Geochim. Geophys. Geosyst.* **3**, 10.1029/2001GC000200 (2002).

29. Stuiver, M. *et al.* INTCAL98 Radiocarbon age calibration 24,000–0 cal BP. *Radiocarbon* **40**, 1041–1083 (1998).

30. Guilderson, T., Burckle, L., Hemming, S. & Peltier, W. Late Pleistocene sea level variations derived from the Argentine Shelf. *Geochim. Geophys. Geosyst.* **1**, 10.1029/2000GC000098 (2000).

31. Bard, E. Correction of accelerator mass spectrometry ¹⁴C ages measured in planktonic foraminifer: Paleoceanographic implications. *Paleoceanography* **3**, 635–645 (1988).

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Correspondence and requests for materials should be addressed to R.T. (e-mail: thunell@geol.sc.edu)

Group decision-making in animals

L. Conradt & T. J. Roper

School of Biological Sciences, University of Sussex, Brighton BN1 9QG, UK

Groups of animals often need to make communal decisions, for example about which activities to perform¹, when to perform them^{2–9} and which direction to travel in^{1,6,7}; however, little is known about how they do so^{10–12}. Here, we model the fitness consequences of two possible decision-making mechanisms: ‘despotism’^{6,7,10} and ‘democracy’^{1,6,7,10}. We show that under most conditions, the costs to subordinate group members, and to the group as a whole, are considerably higher for despotic than for

democratic decisions. Even when the despot is the most experienced group member, it only pays other members to accept its decision when group size is small and the difference in information is large. Democratic decisions are more beneficial primarily because they tend to produce less extreme decisions, rather than because each individual has an influence on the decision *per se*. Our model suggests that democracy should be widespread and makes quantitative, testable predictions about group decision-making in non-humans.

Notwithstanding extensive literature on decision-making by animals acting alone^{13–15}, group decision-making processes have been largely neglected from a theoretical point of view^{6,7,10}. Two extreme mechanisms whereby a group could in principle reach communal decisions are: (1) despotically, where one dominant decides; and (2) democratically, where a majority of group members decides. The relative fitness consequences of these mechanisms are unknown. Many authors have assumed despotism without testing^{6,7,10}, because the feasibility of democracy, which requires the ability to vote and to count votes, is not immediately obvious in non-humans. However, empirical examples of ‘voting’ behaviours include the use of specific body postures^{1,10,11}, ritualized movements^{6,7,9,11,16}, and specific vocalizations^{5,8,12}, whereas ‘counting of votes’ includes adding-up to a majority of cast votes^{5–8,11}, integration of voting signals until an intensity threshold is reached^{9,16} and averaging over all votes^{1,12,16} (Table 1). Thus, democracy may exist in a range of taxa and does not require advanced cognitive capacity. Here, we model the fitness consequences of despotic and democratic decisions. One important context in which social animals frequently have to make communal decisions is in the duration of group activities^{1–7,17}. This ‘activity synchronization’ is essential if a group is to remain spatially coherent^{1–7,10}. However, to reach consensus decisions about the duration of activities, group members often have to compromise their own optimal activity budgets^{1,3,18,19}, the costs of which (synchronization costs) can be an important factor in shaping the social organization of populations^{1–4,17}. Our model compares the synchronization costs of despotic and democratic groups.

The model in Box 1 shows that synchronization costs are usually higher for despotic than for democratic groups. However, if synchronization costs are asymmetric (that is, stopping too late costs less than stopping too early, or vice versa), a modified democratic decision is least costly. In this case, the decision should be based not on a 50% majority, but on a proportion of members that depends on the degree of asymmetry in costs. For example, if stopping too early is twice as costly as stopping too late, the group

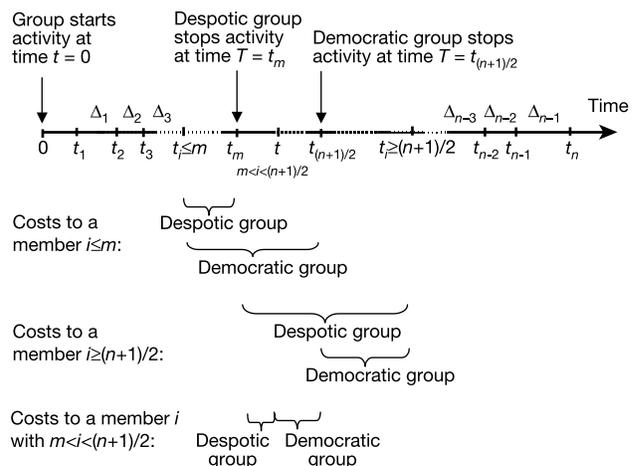


Figure 1 Scheme of a despotic or democratic decision about the duration of a single group activity session, and resulting costs. (See Box 1 for definitions.)

Box 1

Model of synchronization costs

A synchronized^{3-6,17} group of n individuals starts an activity session together at time $t = 0$. The group has to decide when to stop the activity. Each member has its own optimal stopping time^{1-4,19,22} t_1, t_2, \dots, t_n (Fig. 1). A democratic group stops when a majority of members wants to stop; that is, at time $T = t_{(n+1)/2}$. A despotic group stops when the despot (member m) wants to stop (time $T = t_m$). Assuming that (1) synchronization costs increase linearly with the difference between a member's optimal and the group's realized activity duration; and (2) costs of stopping too late or too early are symmetrical. Then the costs to a member $i < (n + 1)/2$ in a democratic group are:

$$C_i = c \sum_{j=i}^{(n-1)/2} \Delta_j \quad (1)$$

where $\Delta_i = t_{(i+1)} - t_i$ for $i < n$ (Fig. 1), and c is a constant 'cost per time'. The costs to members $i \geq (n + 1)/2$ and to despotic members are analogous. Thus, the total costs to a democratic group (C_{dg}) are:

$$C_{dg} = c \left[\sum_{i=1}^{(n-1)/2} \sum_{j=i}^{(n-1)/2} \Delta_j + \sum_{i=(n+3)/2}^n \sum_{j=i-1}^{i-1} \Delta_j \right] \\ = c \left[\sum_{i=1}^{(n-1)/2} i \Delta_i + \sum_{i=(n+1)/2}^{n-1} (n-i) \Delta_i \right] \quad (2)$$

and to a despotic group (C_m):

$$C_m = c \left[\sum_{i=1}^{m-1} \sum_{j=i}^{m-1} \Delta_j + \sum_{i=m+1}^n \sum_{j=m}^{i-1} \Delta_j \right] = c \left[\sum_{i=1}^{m-1} i \Delta_i + \sum_{i=m}^{n-1} (n-i) \Delta_i \right] \quad (3)$$

The costs are higher in a despotic than a democratic group if:

$$c \sum_{i=m}^{(n-1)/2} (n-2i) \Delta_i > 0 \text{ for } m < (n+1)/2 \quad (4)$$

and analogously for $m \geq (n + 1)/2$. As $(2i - n) > 0$ for $i \geq (n + 1)/2$ and $(n - 2i) > 0$ for $i \leq (n + 1)/2$ (except if $m = (n + 1)/2$), it follows that synchronization costs are always higher for despotic than democratic groups.

Relaxing assumption (1), costs are still higher for despotic than for democratic groups in most cases (see Supplementary Information for mathematical details and some exceptions). Relaxing assumption (2) (that is, cost per time $c_{\text{too early}} \neq c_{\text{too late}}$), a modified democratic decision is least costly, in which a proportion, $x = c_{\text{too early}} / (c_{\text{too late}} + c_{\text{too early}})$, of members decides instead of the usual 50% majority (see Supplementary Information).

should stop the activity when two-thirds of its members want to stop. Members that want to stop late should be twice as motivated to influence the decision as members that want to stop early, so integration of voting signals might be the best 'counting of votes' mechanism. Modified democratic decision-making mechanisms are comparable to the tradition, in many human societies, of using a two-thirds majority rather than a 50% majority for decisions that are potentially more costly if taken than if not taken (for example, constitutional changes in Germany²⁰).

The lower costs to a democratic group as a whole imply that democratic decisions are primarily beneficial because they lead to less extreme decisions than despotic decisions (Fig. 1), apart from the advantage that individual members obtain by influencing the decision in their favour. As synchronization costs can accumulate over consecutive sessions of group activities³, the difference in costs between despotic and democratic groups could become quite substantial¹⁻⁴.

The distribution of synchronization costs between group members depends on how homogeneous members are with respect to their optimal time budgets (Box 2). The despot, of course, always pays lower costs in a despotic group. In a homogeneous group, all other members benefit from a democratic decision. This is not true for extremely heterogeneous groups, but even here most of the members benefit from democracy.

No assumptions were made in our model about the means of enforcing a despotic decision (for example, coercion, manipulation or persuasion). However, it is obvious that a despot should not invest more energy than it can gain from despotism. Equally, subordinates should not invest more energy in resisting a despot than they can gain from a democratic decision. Our model suggests that, although single subordinates should not invest as much energy into resistance as the despot is prepared to invest into imposing the decision, all subordinates together should always invest more energy than the despot (Box 2). This suggests that despotic communal decisions might be rare. However, several like-minded members could join forces, make decisions between themselves democratically, but coerce the rest of the group. The result would be an oligarchy¹⁰ (for example, voting is often restricted to adults; Table 1).

Individuals might have incomplete information about their own optimal activity durations because they have imperfect knowledge about their environment (for example, the status of feeding patches, predation risks) and thus, do not exactly know the value to themselves of stopping an activity slightly earlier or later²¹. In

Table 1 Examples of democratic decisions in social animals

Decision	Species	Voting behaviour	Decision mechanism	N	Result
AC	Red deer (<i>Cervus elaphus</i>)	Standing up	Majority of adults decides	10	Group moves when mean 62% (s.d. 8%) of adults stand up*
AC	Gorilla (<i>Gorilla gorilla</i>)	Calling	Majority of adults decides	28	Group moves when median 65% (range 43–86%) of adults call ⁶
AC	Guinea baboons (<i>Papio papio</i>)	Movements	Majority decides	–	Anecdotal report ⁶
AC	Hamadryas baboons (<i>P. hamadryas</i>)	Movements	Majority decides	–	Anecdotal report ⁶
AC	Howler monkeys (<i>Alouatta palliata</i>)	Movements	Majority decides	–	Anecdotal report ⁷
AC	African elephant (<i>Loxodonta africanus</i>)	Low-frequency grumbles	Majority of adult females decides	–	Anecdotal report ⁸
AC	Whooper swans (<i>Cygnus cygnus</i>)	Head movements	Intensity of signals reaches threshold	54	Group flies when signalling intensity ≥ 26.7 signals min^{-1} (ref. 9)
DT	African buffalo (<i>Syncerus caffer</i>)	Direction of gaze	Mean of votes of adult females	13	Average angular difference between mean gazing direction and group travel direction = 3° (range 0–9°) ¹
DT	Hamadryas baboons (<i>P. hamadryas</i>)	Position on resting rock	Majority of adult males decides	155	In 131 of 155 observations the travel direction equalled the majority vote ¹¹
DT	Yellow baboons (<i>P. cynocephalus</i>)	Body orientation	Adults decide	–	Anecdotal report ¹⁰
DT	White-faced capuchins (<i>Cebus capucinus</i>)	Calls	Direction changes continuously with each caller	–	Anecdotal report ¹²
CN	Honeybees (<i>Apis mellifera</i>)	Dances	Integration of signals	–	A complex weighing of voting intensities and number of voters; authors provide a large data set in support ¹⁶

AC, activity change; CN, choice of nest site; DT, direction of travel; N, number of observations.

*L.C., unpublished data.

Box 2

Distribution of costs between members

In a homogeneous group⁴, each member (including the despot) is equally likely to be on any one occasion member 1, 2, ..., *n* who wants to stop the activity session 1st, 2nd, ..., *n*th. Thus, in a democratic group, the expected costs to each member are 1/*n*th of the total group costs (Box 1, equation (2)). In a despotic group, the expected group costs are 1/*n*∑_{*m*=1}^{*n*} *C_m* (Box 1). None of these costs is paid by the despot, but they are equally shared by the (*n* - 1) subordinate members. Thus, a subordinate member benefits by a democratic decision, if:

$$\frac{2c}{n(n-1)} \sum_{i=1}^{n-1} i(n-i)\Delta_i > \frac{c}{n} \left[\sum_{i=1}^{(n-1)/2} i\Delta_i + \sum_{i=(n+1)/2}^{n-1} (n-i)\Delta_i \right]$$

$$\Rightarrow \sum_{i=1}^{(n-1)/2} \frac{n-2i+1}{n-1} i\Delta_i + \sum_{i=(n+1)/2}^{n-1} \frac{2i-n+1}{n-1} (n-i)\Delta_i > 0 \quad (5)$$

This inequality is always true (compare to Box 1, equation (4)).

In an extremely heterogeneous group^{4,22}, the same member is always member 1, 2, ..., or *n* who wants to stop 1st, 2nd, ..., or *n*th. The despot is always member *m*. Since the problem is symmetrical, we only consider the case *m* < (*n* + 1)/2. All *m* members for which *t_i* ≤ *t_m* profit by a despotic decision (Fig. 1). However, all (*n* + 1)/2 members for which *t_i* ≥ *t_{(n+1)/2}* profit by a democratic decision. The [(*n* - 1)2 - *m*] members for which *t_m* < *t_i* < *t_{(n+1)/2}* might or might not benefit by a democratic decision, depending on the values of Δ_{*m*}...Δ_{(*n*-1)/2}. Thus, most of the members (at least (*n* + 1)/2 members) always profit by a democratic decision.

The distribution of costs between members can be used to predict the amounts of energy that a despot should invest in coercing a decision, and subordinates in resisting the despot. If costs to the despot plus costs to the subordinate in a democratic group are higher than costs to the subordinate in a despotic group, than the despot can invest more energy in coercion than the subordinate in resistance. This is usually the case (see Supplementary Information). However, all subordinates together can always invest more energy in resistance than the despot in coercion, because democratic group costs are always lower than despotic group costs (Box 1).

such a case, a group might be 'led' by its most experienced member^{6,7,10,21}. However, our model shows that it only pays group members to follow the decision of a more experienced leader, rather than to make the decision democratically, if errors are large relative to differences in optimal activity durations between members, group size is small, and the difference in experience between leader and ordinary group members is so large that the leader's average error is lower than the average median error of all other group members (Box 3).

The current shortage of studies of group decision-making processes in animals is due to a lack of testable, well-structured concepts and hypotheses relating to group decisions^{5-7,10,11,21}. Our model suggests that democratic decisions, being more beneficial than despotic decisions in most circumstances, should be widespread in animals. It also makes concise, testable and quantitative predictions about when groups should make decisions democratically; which proportion of group members should constitute the critical threshold for a decision, if costs are skewed; what the expected decision results are (for example, mean or median of voting members' requirements); which group members should try to leave democratic or despotic groups; how much members should invest into coercion or resistance to coercion of decisions; when to expect oligarchies; when to expect an experienced leader as decision maker; and which 'counting of votes' mechanism to expect in a particular case. □

Box 3

Groups with incomplete information

We assume that members make a random error, ε_{*i*}, when they determine their own optimal activity duration *t_i*, so that member *i* assumes its optimal activity duration to be *t_i*' = *t_i* + ε_{*i*}; where ε_{*i*} is normally distributed with mean 0 and variance σ_{*i*}². One member (the potential leader; σ_{*l*}) is more experienced than other members (σ_{*om*}) thus σ_{*l*}² < σ_{*om*}². Decisions are made either despotically by the leader or democratically. Errors are either relatively small (|ε_{*i*}| ≪ Δ_{*j*} for *i* = 1, ..., *n*, *j* = 1, ..., *n* - 1), or large (|ε_{*i*}| ≫ Δ_{*j*} for *i* = 1, ..., *n*, *j* = 1, ..., *n* - 1). A despotic group stops the activity session at time *T* = *t_l*' = *t_l* + ε_{*l*}, and the expected group costs are (using equations (3) and (5)):

$$2c/n \sum_{i=1}^{n-1} i(n-i)\Delta_i + c/n \sum_{m=1}^n [(m-1)\epsilon_l - (n-m)\epsilon_l] + c|\epsilon_l|$$

$$= 2c/n \sum_{i=1}^{n-1} i(n-i)\Delta_i + c|\epsilon_l| \quad (6)$$

If errors are relatively small, the sequence with which members want to stop the activity is not different from the sequence of their optimal stopping times *t_i*. Thus, a democratic group stops at time *T* = *t_{(n+1)/2}*' = *t_{(n+1)/2}* + ε_{(*n*+1)/2}. A group would benefit from a leader decision if (using equations (2), (5) and (6)):

$$c/n \left[\sum_{i=1}^{(n-1)/2} (n-2i)\Delta_i + \sum_{i=(n+1)/2}^{n-1} (2i-n)(n-i)\Delta_i \right] + c|\epsilon_l| - c|\epsilon_{om}|$$

$$< 0 \quad (7)$$

As |ε_{*i*}| ≪ Δ_{*j*}, this equality is always false (compare to equation (5)).

If errors are relatively large, the sequence in which members want to stop the activity will depend mainly on the errors that they make. Thus, a democratic group is mainly influenced by the median error of all its members. As |ε_{*i*}| ≫ Δ_{*j*}, a group benefits from a leader decision, if:

$$c|\epsilon_l| < c|\text{median}(\epsilon_{om})| \Rightarrow 0.8\sigma_l < 0.8\frac{\sqrt{5}\sigma_{om}}{\sqrt{n}} \quad (8)$$

This inequality is true, if group size *n* is small and the median error of *n* inexperienced members is higher than the error of the one experienced leader.

Methods

Model of synchronization costs

We modelled the duration and resulting synchronization costs of a group activity session for despotic and democratic groups (Box 1 and Fig. 1). Optimal activity duration generally varies between members^{1-4,19,22}, so groups have to reach communal decisions about group activity duration¹⁻⁷. In a despotic group, group activity duration equals the optimal activity duration of the deciding despot, whereas a democratic group will stop the group activity when the number of members that want to stop reaches a majority. Individual members pay synchronization costs that increase with the difference between the actual group activity duration and the activity duration that would have been optimal for themselves^{1-4,22}.

Distribution of synchronization costs between members

In Box 2 we consider two extremes, namely: (1) all adult group members have similar time budgets⁴ (homogeneous group); or (2) all members differ so widely in their time budgets that there is no overlap in optimal stopping times between members^{4,22} (extremely heterogeneous group).

Groups with incomplete information

In Box 3, the costs to a group with an experienced leader are compared to those of a democratic group. We only consider homogeneous groups, because members mainly profit from an experienced leader if they are similar to it in their time budget requirements⁴. Two extreme cases are investigated: (1) errors are small; and (2) errors are large, relative to differences in optimal timing between members.

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1. Prins, H. H. T. *Ecology and Behaviour of the African buffalo* (Chapman & Hall, London, 1996).
2. Cote, S. D., Schaefer, J. A. & Messier, F. Time budgets and synchrony in activity in muskoxen: the influence of sex, age and season. *Can. J. Zool.* **75**, 1628-1635 (1997).
3. Conradt, L. Could asynchrony in activity between the sexes cause inter-sexual social segregation in ruminants? *Proc. Roy. Soc. B* **265**, 1359-1363 (1998).

4. Ruckstuhl, K. E. To synchronise or not to synchronise: a dilemma for young bighorn males? *Behaviour* **136**, 805–818 (1999).
5. Stewart, K. J. & Harcourt, A. H. Gorillas vocalizations during rest periods—signals of impending departure. *Behaviour* **130**, 29–40 (1994).
6. Byrne, R. W. *On the Move* (eds Boinski, S. & Garber, P. A.) 491–518 (Univ. Chicago Press, Chicago, 2000).
7. Milton, K. *On the Move* (eds Boinski, S. & Garber, P. A.) 357–418 (Univ. Chicago Press, Chicago, 2000).
8. Poole, J. H., Payne, K., Langbauer, W. R. & Moss, C. J. The social contexts of some very low-frequency calls of African elephants. *Behav. Ecol. Sociobiol.* **22**, 385–392 (1988).
9. Black, J. M. Preflight signalling in swans—a mechanism for group cohesion and flock formation. *Ethology* **79**, 143–157 (1988).
10. Norton, G. W. *Primate Ecology and Conservation* (eds Else, J. G. & Lee, P. C.) 145–156 (Cambridge Univ. Press, Cambridge, 1986).
11. Stolba, A. *Entscheidungsfindung in Verbaenden von Papio hamadryas*, 77–80. Thesis, Univ. Zurich (1979).
12. Boinski, S. & Campbell, A. F. Use of trill vocalizations to coordinate troop movement among white-faced capuchins—a 2nd field-test. *Behaviour* **132**, 875–901 (1995).
13. Stephens, D. W. & Krebs, J. R. *Foraging Theory* (Princeton Univ. Press, Princeton, New Jersey, 1986).
14. Krebs, J. R. & Kacelnik, A. *Behavioural Ecology: an Evolutionary Approach*, 3rd edn (eds Krebs, J. R. & Davies, N. B.) 105–136 (Blackwell, Oxford, 1991).
15. Cuthill, I. C. & Houston, A. I. *Behavioural Ecology: an Evolutionary Approach*, 4th edn (eds Krebs, J. R. & Davies, N. B.) 97–120 (Blackwell, Oxford, 1997).
16. Seeley, T. D. & Buhrman, S. C. Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* **45**, 19–31 (1999).
17. Conradt, L. & Roper, T. J. Activity synchronization and social segregation: a model. *Proc. Roy. Soc. B* **267**, 2213–2218 (2000).
18. Decastro, J. M. & Decastro, E. S. Spontaneous meal patterns of humans—influence of the presence of other people. *Am. J. Clin. Nutr.* **50**, 237–247 (1989).
19. Gompper, M. E. Sociality and asociality in white-nosed coatis (*Nasua narica*): foraging costs and benefits. *Behav. Ecol.* **7**, 254–263 (1996).
20. Grundgesetz fuer die Bundesrepublik Deutschland (BGB1. I S.1-1822, 1949).
21. Wagenknecht, E. *Der Rothirsch* (Ziemsen, Wittenberg Lutherstadt, Germany, 1980).
22. Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. *Red Deer: Behaviour and Ecology of two Sexes* (Univ. Chicago Press, Chicago, 1982).

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Correspondence and requests for materials should be addressed to L.C. (e-mail: l.conradt@sussex.ac.uk).

Larval stages of a living sea lily (stalked crinoid echinoderm)

Hiroaki Nakano*†, Taku Hibino†‡, Tatsuo Oji§, Yuko Hara‡ & Shonan Amemiya*‡

* Department of Integrated Biosciences, Graduate School of Frontier Sciences, University of Tokyo, Bldg. FSB-501, 5-1-5 Kashiwanoha, Kashiwa, Chiba, 277-8562, Japan

‡ Department of Biological Sciences; and

§ Department of Earth and Planetary Science; Graduate School of Science, University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo, 113-0033, Japan

† These authors contributed equally to this work

The embryos and larvae of stalked crinoids, which are considered the most basal group of extant echinoderms^{1,2}, have not previously been described. In contrast, much is known about the development of the more accessible stalkless crinoids (feather stars)³, which are phylogenetically derived from stalked forms⁴. Here we describe the development of a sea lily from fertilization to larval settlement. There are two successive larval stages: the first is a non-feeding auricularia stage with partly longitudinal ciliary bands (similar to the auricularia and bipinnaria larvae of

holothurian and asteroid echinoderms, respectively); the second is a doliolaria larva with circumferential ciliary bands (similar to the earliest larval stage of stalkless crinoids). We suggest that a dipleurula-type larva is primitive for echinoderms and is the starting point for the evolution of additional larval forms within the phylum. From a wider evolutionary viewpoint, the demonstration that the most basal kind of echinoderm larva is a dipleurula is consistent with Garstang's auricularia theory⁵ for the phylogenetic origin of the chordate neural tube.

Ripe males and females of the sea lily *Metacrinus rotundus* were collected by fishnet from a depth of 100–150 m in Suruga Bay, Japan, on 22 September 1998 (specimens 1) and 20 September 2000 (specimens 2), and in Sagami Bay, Japan, on 27 September 2002 (specimens 3). The crinoids were transferred to a laboratory aquarium (at 14 °C), where the females spawned at about 19:00 on the date of collection. The eggs were fertilized by sperm obtained by dissecting the testes of a ripe male. The fertilized eggs developed into cleavage stage embryos, but the embryos from specimens 1 and 3 ceased development at this stage. Embryos derived from specimens 2 developed into larval stages.

The unfertilized eggs, which have a diameter of $350 \pm 9 \mu\text{m}$ (mean \pm s.d., $n = 30$) are pale yellow, opaque, and slightly lighter than seawater. The fertilized eggs elevate a conspicuous rough

