of the group[5]. The large mandibular canal suggests the possibility that kollikodontids, like other monotremes, had a bill and/or electrosensory organs at the front of the face. The large size of both *K. ritchiei* and *S. galmani*, which are among the largest Mesozoic mammals known, may reflect the cold conditions of southeastern Australia in the early Cretaceous[18].

Kollikodon ritchiei was a platypus-size monotreme that fed on material that needed crushing but not shearing. Similar adaptations are evident in marine predators, such as sea otters, crabs and some fish that feed on hard-shelled animals. ☐

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Continual change in mate preferences

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SECONDARY sexual characters are highly variable both within[1] and between species[2–6]. Closely related species often differ markedly in sexual morphology but hardly at all in non-sexual traits[2–5]. Here we show that Fisher's runaway process of sexual selection is intrinsically unstable and naturally leads to continual change in sexual traits. Runaway leads to semi-stable exaggeration of female preference for a male sexual character, followed by a slow decay of both traits until runaway is triggered again in a different direction. The process then repeats itself resulting in continual change in male sexual traits through time. Allopatric populations are thus expected to diverge without drift or substantial changes in selective pressures. If there is significant mutation bias acting on the male trait, continual change stops and a stable equilibrium appears. Such an outcome is more likely when exaggeration of the male sexual trait signals good genes.

Let t be a male trait used by females in mate choice and p be the strength of female preference. We assume that both t and p are sex-limited and have a polygenic basis. The per generation change in the mean values caused by Fisher's runaway process is

$$\begin{pmatrix}\Delta\bar{t}\\ \Delta\bar{p}\end{pmatrix}=\frac{1}{2}\begin{pmatrix}G_t & B\\ B & G_p\end{pmatrix}\begin{pmatrix}\beta_t\\ \beta_p\end{pmatrix}+\begin{pmatrix}-u\\ 0\end{pmatrix} \qquad (1)$$

where G_t and G_p are additive genetic variances of t and p, respectively, B is the additive genetic covariance between these two traits, and u measures any biased mutation acting on the male trait[7]. The effect of selection is given by selection gradients (β_p, β_t) evaluated at the population means using an assumption of weak selection[8]

$$\beta_p=\frac{\partial}{\partial p}\ln W_{\mathrm{f}},\qquad \beta_t=\frac{\partial}{\partial t}\ln W_{\mathrm{m}},$$
$$W_{\mathrm{f}}=\exp(-bp^2),\qquad W_{\mathrm{m}}=\exp\left(a\bar{p}(t-\bar{t})-ct^4\right) \qquad (2)$$

where W_{f} and W_{m} are individual female and male fitness, respectively. Female fitness is determined by the strength of preference. We assume that female costs are minimized when there is no discrimination ($p=0$) and increase symmetrically with the strength of preference at a rate b. Male fitness is the product of mating success and survivorship. Mating success is determined by female mate preference. Mean female preference can be either for males with larger ($\bar{p}>0$) or smaller ($\bar{p}<0$) than average trait values[7]. The optimal expression of the male trait under natural selection occurs when $t=0$. Unlike previous models[7–9], male survival is assumed to decrease with the fourth power rather than a quadratic. This is more in line with Fisher's[10] original assumption that the cost of the male trait is very small around the optimum but increases very quickly beyond a certain limit. The coefficients a and c calibrate these two selective effects.

Figure 1 shows an evolutionary trajectory generated by the model. The population starts near the origin, where females show no preference ($\bar{p}=0$) and males have a trait value that achieves maximum survivorship ($\bar{t}=0$). It quickly evolves away from the origin in a runaway process[9,10]. The system converges to a curve, on which evolutionary change slows down, but does not stop completely. Here the male trait is exaggerated and females show corresponding strong preference. Female preference then slowly declines until runaway starts again but this time in a negative direction. This negative runaway stops when the system converges on another semi-stable branch at which t and p are negatively exaggerated. Then a very slow movement in a positive direction starts until runaway is triggered toward positive values.

The evolutionary trajectory can be studied further by decomposition into fast and slow dynamics[11,12]. Runaway, or the fast dynamics, is given by neglecting the cost to female mate preference b and mutation bias u that are assumed to be much smaller than the other parameters[11,12]

$$\Delta\bar{p}=\frac{B}{2}\left(a\bar{p}-4c\bar{t}^3\right),$$
$$\Delta\bar{t}=\frac{G_t}{2}\left(a\bar{p}-4c\bar{t}^3\right). \qquad (3)$$

Setting $\Delta\bar{p}=\Delta\bar{t}=0$ yields a curve of the equilibria for the fast dynamics (red line in Fig. 1). We can distinguish a stable (solid) and unstable (dashed) part of the curve[9,13,14]. Points B and D are the two points where the slope of the curve of equilibria is the same as the slope of the fast dynamics trajectory, $\Delta\bar{p}/\Delta\bar{t}$. The subarc between B and D is unstable and the two branches outside are stable.

Evolution near the curve of equilibria is given by the slow dynamics which includes the effects of b and u. The per generation change in mate preference is (see appendix 2 of ref. 11)

$$\Delta\bar{p}=\frac{G_p}{2}\left(-2b\bar{p}+ua\right). \qquad (4)$$

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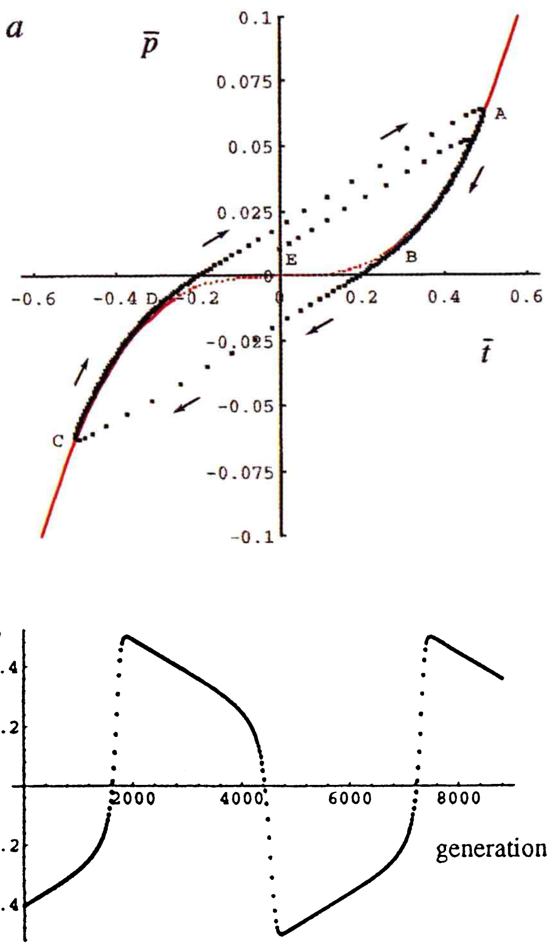

FIG. 1 Cyclic evolution caused by Fisher's runaway process is plotted as *a*, the joint evolution of the mean female preference ($\bar{p}$) and mean male trait ($\bar{t}$) and *b*, as change in the mean male trait ($\bar{t}$) per generation. The population is plotted every 20 generations. As in previous models[11,12] we simplify the dynamics by a decomposition into fast and slow dynamics. This is justified on the assumption that mutation bias *u* and the cost to female mate preference *b* are both much smaller than the other parameters. We also make a weak selection assumption that the fitness coefficients *a* and *c* are both smaller than the additive genetic variances G_t and G_p which are of order unity (that is, $b, u \ll a, c \leqslant G_t, G_p \approx O(1)$). We make the simplifying assumption of constant genetic variance. Under these conditions, the additive genetic covariance between the male trait and female preference converges quickly to $B = aG_tG_p/2$ (ref. 11). The fast dynamics (ignoring *b* and *u*) define a curve of the equilibria (red line) $\bar{p} = 4c\bar{t}^3/a$, which is unstable (dashed line) when its slope $12c\bar{t}^2/a$ is less than that of the evolutionary trajectory during runaway $B/G_t = aG_p/2$, but otherwise stable (solid line). Once close to the curve of equilibria, the evolutionary trajectory is given by the slow dynamics (including *b* and *u*) which causes movement along the curve of equilibria. The points A and B define the transition between runaway and the slow dynamics $(\bar{p}_A, \bar{t}_A) = (2a^2G_p^{3/2}/3\sqrt{6c}, aG_p^{1/2}/\sqrt{6c})$ and $(\bar{p}_B, \bar{t}_B) = (a^2G_p^{3/2}/2\sqrt{6c}, aG_p^{1/2}/2\sqrt{6c})$. As the model is symmetrical, points C and D are found by changing the sign of A and B. In this simulation, mutation bias was set to zero, so the equilibrium point E lies at the origin and is unstable. Parameter values are $a = 0.4$, $b = 0.001$, $c = 0.05$, $G_t = 0.5$, $G_p = 0.5$, $u = 0$.

Change in the male trait is now purely a function of the mean preference and follows $\bar{t} \approx (a\bar{p}/4c)^{1/3}$. These equations describe movement along the stable branches of the equilibrium curve towards equilibrium at point E

$$(\bar{p}_E, \bar{t}_E) = \left(\frac{ua}{2b}, \left(\frac{ua^2}{8bc}\right)^{1/3}\right). \qquad (5)$$

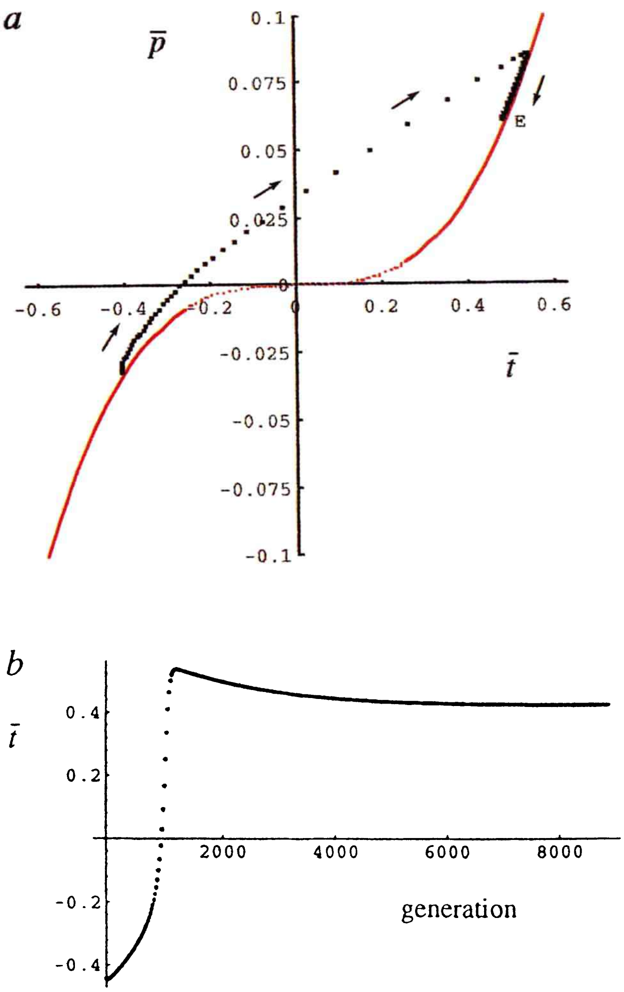

FIG. 2 Stable evolution caused by Fisher's runaway process. In this example mutation bias on the male trait *u* is large enough and the cost of choice *b* small enough for $\bar{p}_B < ua/2b$. So the equilibrium point E lies on the stable arc of the equilibrium curve and is globally stable. Parameter values are $a = 0.4$, $b = 0.001$, $c = 0.05$, $G_t = 0.5$, $G_p = 0.5$, $u = 0.001$.

Stability depends on whether E lies on a stable branch of the equilibrium curve. If $\bar{p}_E > \bar{p}_B$, the population smoothly converges on the equilibrium which is globally stable (Fig. 2). But if $\bar{p}_E < \bar{p}_B$, then the fast dynamics takes the population away from the equilibrium once it reaches point B and the equilibrium E is never reached (Fig. 1). This conforms to the Poincare–Bendixon theorem that a two-dimensional autonomous system with a single unstable equilibrium has a cyclic trajectory if the system is confined to a finite area[15].

If mutation bias is negligibly small ($u = 0$), which is likely to be the case in many sexual traits, there is an unstable equilibrium at the origin. The male trait cycles between positive and negative values and the time between successive runaways derived from equation (4) is $\tau \propto 1/bG_p$. As the cost to female mate preference *b* is assumed to be small, male traits can persist for many generations. The time period during which a runaway occurs is very much shorter than τ and is unaffected by *b* (see equation (3)).

If *u* is positive, stability depends on a number of other parameters. Of particular importance is the cost of mate preference *b*. If *b* is large compared to *u*, the equilibrium is unstable. The population traces the same trajectory as when $u = 0$. Cyclic behaviour is seen so long as *b* remains greater than the critical value

$$b_c = \frac{6u\sqrt{6c}}{aG_p^{3/2}}. \qquad (6)$$

A further conclusion concerns the magnitude of additive genetic variance. Greater additive variance in female mate preference G_p increases exaggeration, the rate of turnover and stability but has no effect on the location of equilibrium. In contrast, additive variance in the male trait G_t has little impact. It neither affects exaggeration, rate of turnover, stability or the location of equilibrium. G_t only affects the speed of Fisher's runaway process, which occurs in such a short time interval as to be instantaneous in comparison to the interval between successive runaways.

Cyclic evolution is a general property of Fisher's runaway process. The only change we have made to the standard model[7–9] is to make selection on the male trait weak around the natural selection optimum allowing runaway to be initiated and to decrease survival chances rapidly beyond a certain value. We note that strong stabilizing selection at the origin will inhibit runaway but continual evolution follows once runaway occurs[7–9]. Similar instability can be generated in models of the handicap process in which the male trait acts as an indicator of heritable viability, so-called good genes (Y.I., T. Kubo and A.P., manuscript in preparation). But a stable equilibrium is a more common outcome. Mutation bias is known to be strong on viability traits[16,17] and the handicap model assumes that viability traits strongly influence the expression of the male sexual trait[8,12]. As we have seen significant mutation bias is necessary for a stable, non-zero equilibrium.

Current explanations of the diversity of sexually selected traits have stressed the importance of random genetic drift[9,18] and distinct selective pressures in geographically separated populations[19]. Given cyclic evolution, such slight differences affecting selection or genetic parameters (that is, a, b, c, u, G_t or G_p) will cause allopatric populations to fall out of phase quickly and evolve distinct sexual phenotypes. The consequences of this are more easily visualized by increasing the dimensionality of the model to multiple female preferences for different male traits (such as colours, songs or feathers)[11], which greatly increases the number of possible semi-stable states (A.P. and Y.I., manuscript in preparation). The instability of Fisher's runaway process may well explain the high variability of sexual traits between closely related species[2–6]. ☐

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Ejaculate quality and the success of extra-pair copulations in the zebra finch

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In many passerine birds, sperm competition[1,2] is intense and extra-pair paternity frequent[3]. The outcome of sperm competition is often determined by relative sperm numbers[4,5], and theory predicts that males should maximize the number of sperm they ejaculate during extra-pair copulations[6,7]. Differences in sperm quality between males also affect the outcome of sperm competition[4]. Here we report that the swimming velocity of sperm of the zebra finch, *Taeniopygia guttata*, varies predictably within males, and is determined, together with sperm numbers, by the time since last ejaculation. By performing extra-pair copulations outside their own-pair copulation period, males maximize both the quality and number of sperm in ejaculates. These effects are a consequence of the way sperm are stored and mature in the male reproductive tract. The disportionate success of extra-pair copulations[8], also seen in other birds[9], may therefore be explained in terms of the independent effects of sperm numbers and velocity.

When male zebra finches that were rested (that is, had not copulated in the previous 7 days) ejaculated several times in rapid succession into model females[10], the quality of their ejaculates decreased markedly and their sperm store, the seminal glomera[11], became depleted. The average path velocity of sperm, measured using computer-aided sperm analysis (Hobson Sperm Tracker), from two ejaculates one hour apart from each of 13 rested males fell by almost half, from 32.88 ± 4.40 (s.e.) $\mu\text{m s}^{-1}$ to $18.75 \pm 1.95\ \mu\text{m s}^{-1}$ (paired $t_{12} = 3.074$, $P < 0.01$). Five males that ejaculated a mean of 3.20 ± 0.37 times to exhaustion transferred a mean total of $8.05 \times 10^6 \pm 2.95 \times 10^6$ sperm in successively smaller ejaculates (first, $5.29 \times 10^6 \pm 1.56 \times 10^6$; second, $1.91 \times 10^6 \pm 1.17 \times 10^6$; third, $0.75 \times 10^6 \pm 0.44 \times 10^6$; fourth, $0.166 \times 10^6 \pm 0.08 \times 10^6$; two-way analysis of variance (ANOVA) on log $(x+1)$ sperm numbers: male, $F_{4,10} = 7.62$, $P < 0.005$; ejaculate number, $F_{3,10} = 13.91$, $P < 0.001$). A mean of $1.32 \times 10^6 \pm 0.56 \times 10^6$ sperm (16% of the original number, $8.05 \times 10^6 + 1.32 \times 10^6$) was left in their seminal glomera. Thus 84% of the sperm in the seminal glomera of rested males was available for ejaculation. Of the remainder, $79.46\% \pm 8.50$ sperm were morphologically non-normal (senescent) compared with those in ejaculates ($32.27\% \pm 8.20$; paired t-test on arcsin transformed values, $t_4 = 4.41$, $P < 0.02$).

The mechanism responsible for this difference in ejaculate quality was a gradation of sperm quality within the seminal glomera: the velocity of motile sperm ($P < 0.005$), the proportion of motile sperm ($P < 0.03$), and the proportion of morphologically normal sperm ($P < 0.05$) all increased from the most proximal region to that nearest the cloaca (Fig. 1). The velocity of sperm from the cloacal ($33.44 \pm 4.89\ \mu\text{m s}^{-1}$) and mid region ($17.44 \pm 2.09\ \mu\text{m s}^{-1}$) of the seminal glomera did not differ significantly from that in first and second ejaculates, ($t_{21} = 0.084$, $P > 0.1$; $t_{21} = 0.457$, $P > 0.1$, respectively). This gradation of sperm quality is presumably due to a combination of maturation, as in the mammalian epididymis[12,13], and a sorting process.

The temporal consequences of these differences in ejaculate quality were determined by measuring the rate of sperm production (Fig. 2). As the seminal glomera of rested males contain 8.05×10^6 sperm available for ejaculation (above and ref. 14), and sperm are produced at a rate of 1.885×10^6 per day (Fig. 2), recovery of both sperm number and velocity after depletion requires 4–5 days.