

Animal Decision-making and the 'Concorde Fallacy'

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Both animals and humans appear to commit the 'Concorde Fallacy': they seem to gear their investment into a vital task to their past investment, though ideally they should gear it to the net expected future benefits (= benefits minus costs to complete the task)^{1,2}. By uncoupling past investment from expected benefits, animals have been variously shown to behave in a Concordian way, though in some cases alternative explanations are still possible. While there is no firm evidence that such behaviour is maladaptive, for instance due to cognitive constraints, there are at least two reasons why Concordian behaviour might be adaptive rather than 'fallacious'. One is that past investment lowers the prospects of future reproduction, thereby altering net expected benefits; the other is that past investment is indispensable to gathering the information necessary for deciding the least costly course of action, i.e. to reap the greatest benefit.

Humans are by no means always rational when about to make a decision, as shown by the fallacy committed by the constructors of the Concorde plane. When, in the midst of designing the plane, they discovered that the endeavour would run into economic disaster, they went on with construction; they argued that they had already invested many millions of pounds that would be wasted if they gave up. Apparently a similar, irrational sentiment, dubbed the 'Concorde Fallacy', underlay the continuation of the Vietnam War when it was becoming clear the war would be lost; US citizens mourned: 'Our boys must not have died in vain'. Avoidance of the Concorde Fallacy would have saved many lives.

Concordian behaviour in animals

Behavioural ecologists concerned with decision-making in animals soon began to consider whether other animals would be liable to commit the Concorde Fallacy. If natural selection had optimized behaviour^{3,4} the fallacy should clearly be avoided, and

special explanations would be required to account for cases where it was shown to occur.

To survive and reproduce successfully, an animal has to accomplish various tasks (digging a nest hole, tending offspring, etc.). While performing such tasks, the animal incurs costs. In order to avoid the Concorde Fallacy, it would have to compare the costs of two options: to go on completing the task at hand, or to discontinue and start anew. Regardless of what the animal has invested in the past, it should follow the less costly course of action, assuming that the expected final benefit has remained the same.

To invoke past investment (= costs) as instrumental in this decision-making, one would have to demonstrate that (1) an assessment of those costs would be needed for quantitative comparison of the available options, or (2) assessment of those costs would be constrained for cognitive reasons, or (3) the past investment would have changed the expected benefits. Clearly, in cases (1) and (3), Concordian behaviour would be adaptive and only superficially appear fallacious. Case (2) is illustrated by the fact that the Concorde plane is making a profit nowadays, thus justifying the earlier, seemingly imprudent decision to continue its construction; even humans are not omniscient.

Both costs and benefits are ultimately measured in fitness. As a task nears completion, costs accumulate while the expected benefits increase; thus there is a positive correlation between past costs and future benefits. In order to know on which of the two quantities the animal bases its decision, one would have to uncouple them. To foresee the future, even on a preprogrammed basis, is notoriously difficult. Yet there is also a negative correlation between future costs and expected benefits, with the former being perhaps easier to assess because past costs might serve as a yardstick to extrapolate into the future⁵. In this way an animal might indirectly assess future

benefits, without committing the Concorde Fallacy, by capitalizing on information obtained in the past. Behaviour is 'Concordian' when it is based on past investment, regardless of whether the ensuing decision is adaptive.

Manipulation of future benefits

Parental investment has formed one focus of research into investment decision rules. Costs (= past investment) were assessed, for instance, by the size of a clutch produced or the length of time it had been cared for. Future benefits were measured as the number of offspring reaching independence.

In accordance with theory, Pressley⁶ found that three-spined sticklebacks (*Gasterosteus aculeatus*) increased nest defense with brood size, with past investment having apparently remained constant. Yet since brood sizes may have depended on how attractive a male had been, the result could also mean that the better quality males were also the more able defenders.

Manipulation of brood size across randomly chosen subjects is the only way around this impasse. In a study with great tits (*Parus major*), clutch size in an experimental group was reduced to a constant number of four, and past investment in terms of eggs laid and time incubated were kept constant among experimental birds and controls⁷. The period that experimental females had been incubating the altered clutch was negligible in proportion to the pre-manipulation amount of time invested in incubation. [This was unknown for an otherwise similar experiment with red-winged blackbirds (*Agelaius phoeniceus*)⁸, which was therefore possibly confounded by differential energy expenditure in the past⁹.] The great tits were observed to behave prudently: those with reduced clutches invariably reduced their anti-predator harassment against a live pygmy owl (Figs 1 and 2), and defense was not related to previous clutch size. Had the tits behaved in a Concordian manner they should have stuck to their original levels of defense, as demonstrated by the controls (see also Ref. 10).

Unexpectedly, both great tits and red-winged blackbirds fail to dis-

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play anti-predator nest defense in proportion to the number of young. Responses correlate neither with past investment nor with future benefits^{8,11}; this has been corroborated by brood size manipulation experiments with great tits (W. Windt, pers. commun.). Recent theory on the relations between parental investment, parent-offspring conflict and brood size¹² may help to solve this puzzle.

Past investment and its manipulation

Experiments in which only future investment is manipulated cannot settle the question of whether the wastage of past investment is considered by the animal. Therefore, past investment became the focus of a small number of studies.

In the savanna sparrow (*Passerculus sandwichensis*), the potential for re-nesting declines in the course of a short breeding season. In the course of an individual's breeding cycle anti-predator nest defense increased, but markedly only after hatching of the young¹³ (see also Ref. 14). If re-nesting potential were high a bird should refrain from giving the maximum response and vice versa. Later-nesting birds should begin to approach maximum response levels sooner in their breeding cycle than those nesting earlier. It turned out that the number of days before re-nesting potential reached zero did not influence the response markedly. Rather, the stage of nest development and the number of days after re-nesting potential reached zero explained most of the variation in defense behaviour.

From this, Weatherhead¹³ concluded that future prospects of breeding had little influence on parental defense level. The findings are, however, open to at least one other interpretation. In the first half of the breeding cycle, responses were so low that during about half of the time when re-nesting potential declined, the variation of responses was correspondingly low. This may have prevented the expression of any assessment in the first half of the nesting cycle.

In a manipulative study with red-winged blackbirds, past investment was made to vary whilst expected benefits were equalized¹⁵, thus reversing the equal investment-

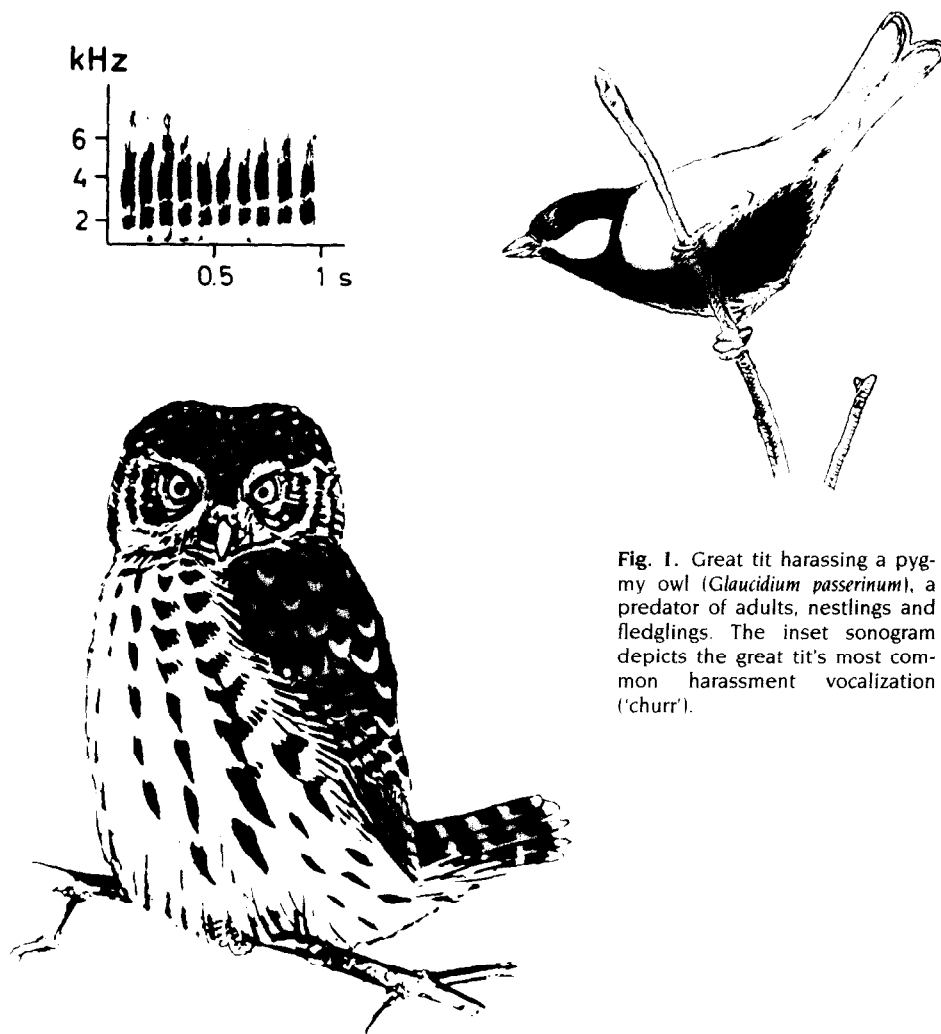


Fig. 1. Great tit harassing a pygmy owl (*Glaucidium passerinum*), a predator of adults, nestlings and fledglings. The inset sonogram depicts the great tit's most common harassment vocalization ('churr').

unequal benefits study with this species (see above). Investment was manipulated by switching clutches of equal size between nests differing in initiation dates, thereby achieving short and long incubation periods in addition to control nests with normal incubation. Females with artificially prolonged incubation can be assumed to have invested more energy when tested with a predator at the nestling stage⁹. While the manipulation did not affect the females' abilities to rear nestlings, the long incubation birds responded more strongly than the short incubation birds, and only during the second half of the nestling period. Thus there seems to be some evidence that the birds were acting in a Concordean fashion.

Two other possibilities come to mind. First, parents are known to increase their parental effort with offspring age because the reproductive value of the offspring increases concomitantly¹⁶. If female blackbirds gauge offspring age by the length of previous incubation the same result would have been obtained. Responses of control and long incubation females support

this interpretation whereas those from the short incubation group do not. The recognition of nestling age by the amount of past investment cannot be general among birds. Pied flycatchers (*Ficedula hypoleuca*) and shama thrushes (*Copsychus malabaricus*), when given nestlings of an inappropriate age, adjust the size of prey fed to them instantaneously (E. Curio, unpublished). This seems to indicate that parents can recognize the age of nestlings independently of their investment in them.

Secondly, by incubating a clutch for longer, a female reduces her potential for re-nesting in the same season, thus curtailing her residual reproductive value. Although re-nesting potential is very low anyhow (P.J. Weatherhead, pers. commun.) the possibility remains that females have optimized parental effort in the long term and not fallen victim to the Concorde Fallacy.

In conclusion, while manipulation of future benefits has yielded results that are compatible with the animal avoiding the Concorde Fallacy, manipulation of past in-

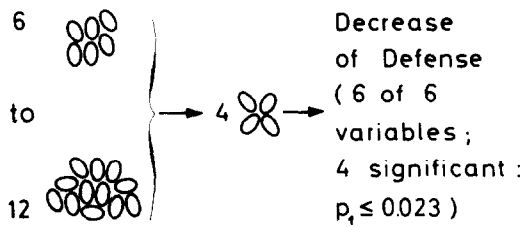


Fig. 2. Clutch size manipulation experiment to study defense behaviour in relation to expected future benefit. Both experimentals ($n = 23$ pairs) and controls ($n = 22$ pairs) had experienced the same past investment (number of eggs, incubation performance); P_1 is one-tailed. Reproduced from Ref. 18, with permission of the Nederlandse Ornithologische Unie.

vestment could not unequivocally demonstrate that animals do commit it. Only further experimental manipulation of past investment would settle the issue.

Problems of cognition

In principle, the difficulties devilling any attempt to sort out the effects of investment and future benefit could stem from constraints on animal cognition. If an animal could not correctly assess, for instance, the number or the quality of its offspring at stake, their future prospects of survival, or its own survival, it could hardly make the correct decision with regard to future benefits.

For example, in a test of the Concorde Fallacy, female great

golden digger wasps (*Sphex ichneumoneus*) were found to defend their nest burrows against usurpers in accordance with their investment in them¹⁷. Investment was measured by the number of katydids individual females had hoarded for larval food. However, the wasps proved unable to count the total number of katydids (i.e. their own plus those of other females) in a burrow and were thus unable to assess expected benefits¹⁷. Furthermore, even in the absence of the constraint on counting ability, nest burrow defense was an inappropriate test of the investment versus expected benefit hypothesis, since defense based solely on expected benefits is not an evolutionarily stable strategy in this situation: if all digger wasps based their decision for giving up a fight on a correct assessment of total burrow contents, random factors would determine the outcome, which clearly would not be stable. For these wasps, the simpler 'rule of thumb' of knowing one's own investment would be superior¹⁷.

Great tits were found not to vary their strength of anti-predator brood defense in relation to weight

of young, though weight of young is a fairly reliable predictor of survival prospects. The possibility thus remains that parents are unable to gauge quality of young¹⁸. A similar difficulty surrounds any conclusion concerning number of young to be fledged. Both red-winged blackbirds and great tits were found not to gear their brood defense to brood size^{7,11}. In the great tit, this cannot be due to a general inability to assess brood size or a factor correlated with brood size, since parents flexibly gear their defense to brood size in second broods, and match their feeding rate to brood size in general¹⁸ (see also Ref. 19).

There are indications that great tit parents feed nestlings with maximum effort, since they cannot increase their feeding rate if brood size is artificially increased. If parents used their feeding performance as a yardstick to adjust their defense level there would be no variation of defense level with brood size, as in fact observed²⁰. This untested maximum effort-defense level hypothesis could also explain the fact that parents of both great tits and red-winged blackbirds gear their level of defense to clutch size only because incubation is energetically much less demanding than feeding nestlings. Should this hypothesis receive support, great tits could be said to behave in a Concordian way: feeding effort appears to be something that needs to be experienced rather than forecast.

The adaptiveness of Concordian behaviour

Animals have more or less fixed budgets²¹, for example for reproducing, and there are trade-offs between early and late reproduction; making a big expenditure on the first bout of reproduction curtails future reproduction^{22,23}.

Based on this concept of the 'cost of reproduction', Sargent and Gross²⁴, developed a model of life-long allocation of parental investment that views Concordian behaviour as part of an optimal life history (Fig. 3). The reproductive success of a current brood (P) is assumed to increase with diminishing returns with present investment, while future reproductive success (F) is assumed to decrease

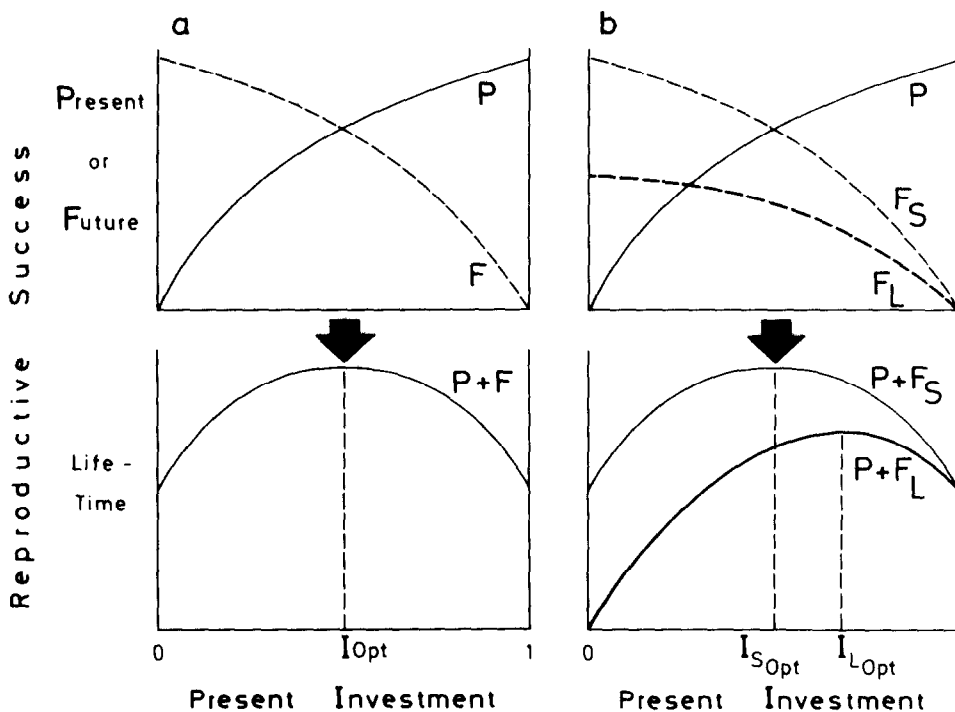


Fig. 3. The effect of present investment into a brood (e.g. defense) on reproductive success. (a) Present reproductive success (P) and future reproductive success (F) determine lifetime reproductive success ($P + F$) as a function of present investment under normal circumstances, with I_{Opt} being the optimal level. (b) Present (P) and future reproductive success, after investing lightly (F_S) or heavily (F_L) into past broods, with an optimal level of lifetime reproductive success being bigger after a large investment ($I_{L_{Opt}}$) than after a smaller investment ($I_{S_{Opt}}$). See text for details. Modified from Ref. 25.

with present investment (Fig. 3a); reproduction is costly. Lifetime reproductive success (= darwinian fitness) is the sum of present and future reproductive success (Fig. 3a: $P + F$). The optimal degree of present investment, that maximizes fitness, is indicated by I_{Opt} . Neither maximum P nor maximum F will yield the highest fitness; rather, intermediate levels of both will do so.

Because reproduction has a cost, heavy investment in the past leads to less expected future reproduction (Fig. 3b: F_L), as compared to a smaller past investment (F_S). Therefore, lifetime reproductive success is optimized at a level of I_{Opt} when investment in the past has been large ($P + F_L$), i.e. by a greater present effort than would have been optimal with smaller past investment ($I_{S_{opt}}$). The animal should thus consider its past investment to the extent that this feeds into its residual reproductive value²⁶. This Concordian behaviour is in effect the prudent weighting of future prospects of reproduction (or any other behaviour subject to these constraints).

By similar considerations it can easily be shown that present investment should grow in proportion to the size of the brood at stake. In a test of the theory, it was found that male bluegill sunfish (*Lepomis macrochirus*), when defending their brood against a model bluegill predator, invested according to both brood size and past investment²⁵. Unfortunately, males with the allegedly heavier past investment, as measured by time spent in brood care, could not be shown to be in lower body condition than males with the reduced investment. Assuming that there have been more subtle costs of reproduction, this experiment is the most convincing evidence that past investment and future benefits influence parental decision-making.

The teasing apart of both factors in a more direct way has made progress. By alleviating the costs great tit parents incur by feeding young, and by manipulating brood size just before a test on present investment, both factors are being manipulated (W. Windt, pers. commun.). All such experiments hinge

on the ability of the animal to monitor its reproductive value, for which there is now good evidence²⁷.

Bayesian decision-making

Concordian behaviour can be adaptive in yet another way; an animal may need time, prior to making a decision, for sampling information about the environment. Any imprudent decisions based on such investment would be regarded as fallacious, not because of being Concordian but because of misjudging the information sampled, i.e. making the wrong prediction from it. To discriminate this type of effect of past investment from the Sargent-Gross²⁴ approach (see above) one would have to show that sampling of information increases rather than decreases reproductive value.

In a recent study²⁸ on mate choice decisions in a gammaridean amphipod (*Gammarus lawrencianus*) it was found that males base their choice of a female with which to copulate on the proximity of the female to copulation day (termed 'female State'). Females become ready for copulation every seven days. A male does best when he contacts a female on the day she becomes receptive; he does worst right upon egg-laying. A male keeps a female in amplexus until copulation day. Tenacity in keeping a female amplexed, an expression of present investment, varies with the number of days since initially amplexing the female for a continuous period (Fig. 4).

To tease apart investment and future benefit, pairs were gently separated 3 h after having formed. The members of a pair were allowed to re-amplex 6 h prior to testing for tenacity. Again, there is a positive relationship between tenacity and the number of days since initially amplexing, reflecting female State (Fig. 4). This demonstrates that females were valued ever more highly as they approached copulation, since the time that the male had spent amplexing with the female was held constant in this experiment. Since the slope, not the intercept, of the curves in Fig. 4 is different, males in the 'interrupted amplexus' experiment systematically underestimate the value of the female, as com-

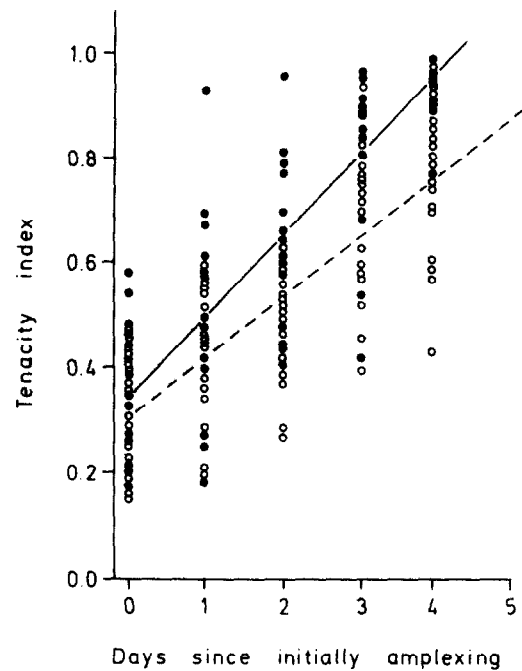


Fig. 4. Present investment into an amplexed female by male amphipods, *Gammarus lawrencianus*, as measured by tenacity to endure osmotic stress, in relation to days since initial amplexus. Solid symbols represent continuous amplexus, open symbols represent interrupted amplexus. Slopes differ significantly ($P < 0.001$). Modified from Ref. 28, with permission from Baillière Tindall.

pared to the continuous amplexus males.

Hunte *et al.*²⁸ contend that the males sample two things: (1) on first contact, female State is assessed, with the uncertainty about

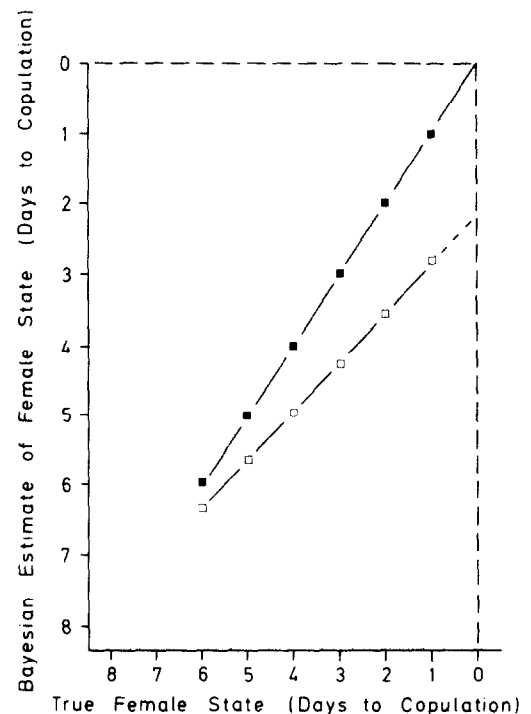


Fig. 5. Computed female States in *Gammarus lawrencianus*, given as Bayesian estimates which allow for the impact of prior, sampled probabilities of female States in the environment, as a function of true female State (= number of days to copulation). Upper line: male certain; lower line: male uncertain (± 2.0 days). Modified from Ref. 28, with permission from Baillière Tindall.

it decreasing as time in amplexus passes; (2) the distribution of females in a given State is assessed before the male goes into amplexus.

Bayes' theorem²⁹ specifies the way an 'ideal' observer would combine the two sources of information to generate an informed final probability distribution of female States. Based on Bayes' theorem and the actual distribution of female States, Hunte *et al.* computed the Bayesian estimate of female State as a function of true female State (Fig. 5). It turns out that with any male uncertainty about the female's State, the male would invariably underestimate her true value as actually observed (Fig. 4).

This result has been accounted for by the existing skew of the distribution of true female States prior to a male's amplexus²⁸, but this need not be so. The mistake a male commits upon contacting a female need *not* be symmetrical about any given female State. Any asymmetry could lead to the observed underestimation of female State and, thus, render the male's prior evaluation of the resource distribution

hypothetical.

The Bayesian approach (Fig. 5) suggests an experiment to which existing data do not speak: the computed curves could be tested by pairing males with females of different known value, to find out whether the males exhibit the predicted levels of tenacity.

Since sampling information about a particular resource and about the distribution of resources optimizes decision-making by increasing, rather than decreasing, reproductive value it is a type of past investment of its own right. Concordian behaviour can therefore be adaptive for two different reasons.

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Announcement summer tropical clearance sale

Western Mesoamerica had a France-worth of tropical dry forest, but today less than 2% remains. Only 0.09% has conservation status. The dry tropical forest in Guanacaste National Park (GNP) in northwestern Costa Rica wants to buy itself, replant itself, and regrow itself. This restoration of 700 km² of dry forest and rainforest refugia will double the amount of conserved dry forest in Mesoamerica.

How to restore it? Give it back the land it once occupied, and protect it from ranching, fires, and hunting. The organisms come from the 302 km² of national park restoration already within GNP and from population fragments in the damaged habitats. Invasion by native organisms will be natural or assisted, depending on the zone. And GNP is also cultural restoration. Its user-friendly performance as a living classroom and research laboratory will be conducted and attended largely by Costa Ricans, with an international audience as well. The Costa Rican government has agreed to match all donations 1:1 with endowment funds. GNP has raised \$2.62 million and needs at least \$1 million more for the small parts. An additional \$4 million is required for the purchase of GNP's 160 km² core. This purchase will secure the entire project.

Please participate in the summer sale - \$300 buys you all of (forever):

1 hectare or 2.47 acres	0.5 parrot	25 spiny pocket mice
0.001 jaguar	5 m riverbank	0.429 insect species
0.1 adult guanacaste tree	0.005 tapir	0.01 white-lipped peccary
0.01 muscovy duck	1 rattlesnake	400 dung beetles
0.0029 herp species	200 orchids	20 toads
0.1 agouti	3,000,000 unlisted organisms	125,000 acorns
0.05 curassow	0.000029 volcano	0.023 mammal species
1,000,000 ants	0.0071 bird species	100 vines
10,000 mushrooms (early rainy season bargain)	0.04 anteater	5,000 bruchid beetles (rainy season purchase not guaranteed)
0.25 tinamou	200 sphinx moth caterpillars (offer good in July only)	100 scorpions
0.4 adult guapinol tree	0.03 spider monkey	0.000028571 peripatus species
0.000016 of the join between 330 km ² dry forest and 210 km ² rainforest		
20,000 m ³ of sunshine, 4,700,000,000 raindrops, 1 hectare of clouds, and some dew		

Your tax-deductible summer purchase order in *any* amount should be mailed to: Nature Conservancy-Guanacaste Fund, 1785 Massachusetts Avenue, NW Washington, DC 20036. All purchases will be held for your on-site inspection by the Costa Rican National Park Service.

Detailed information is available from Daniel H. Janzen, Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104 (215/898-5636) or at Santa Rosa National Park, Apartado 169, Liberia, Guanacaste Province, Costa Rica (country code 506/69-55-98).