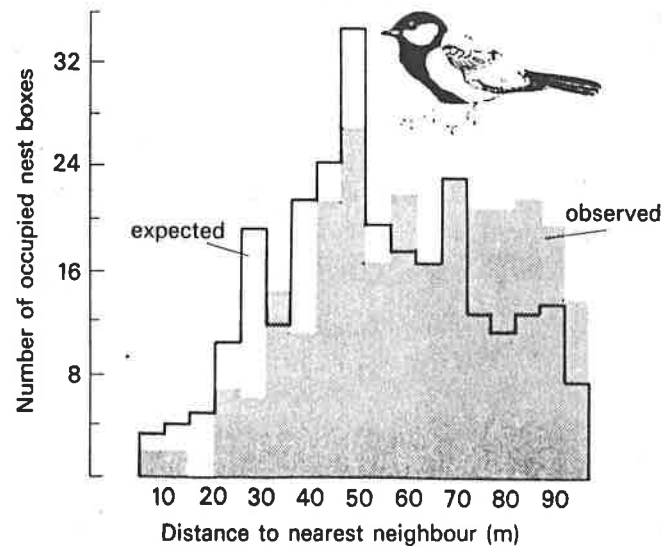
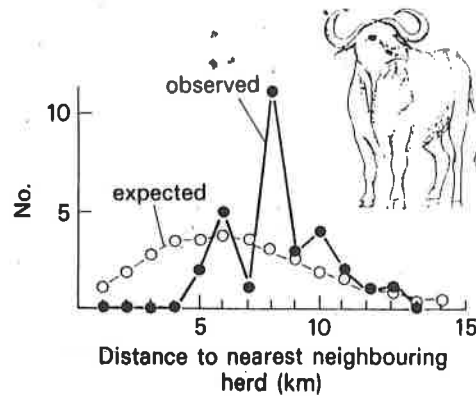


# SPACING OUT = EVIDENCE OF TERRITORIALITY (ECOLOGICAL DEF'n)

(c) Great Tits



(d) Buffalo Herds



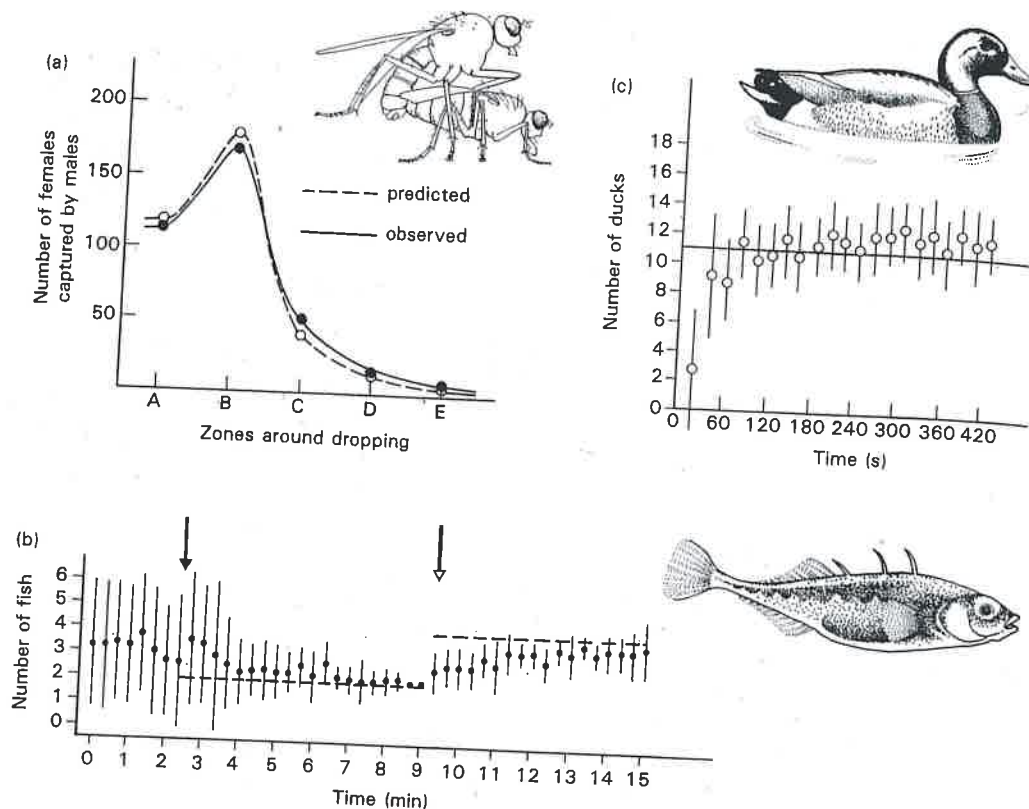
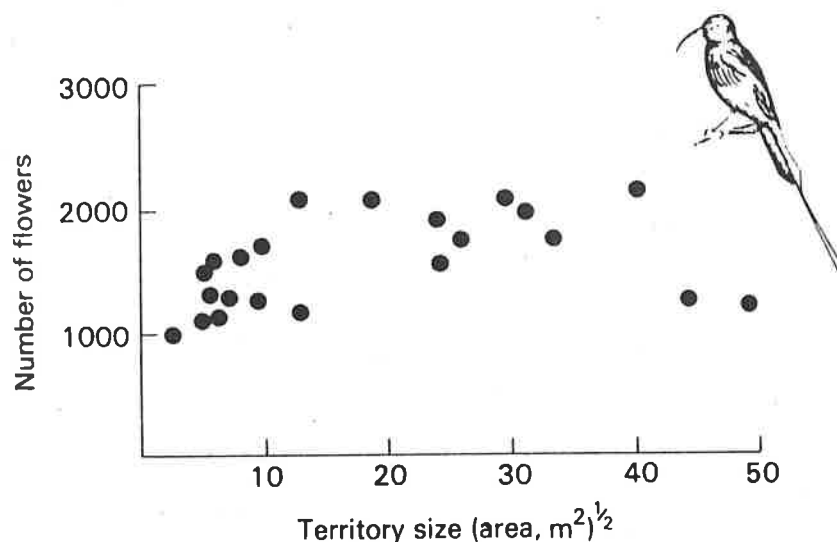


Fig. 5.2 Three examples where input matching appears to occur. (a) Dungflies: the observed number of females captured (●—●) by male dungflies in a series of zones A–E on or around a cow dropping fits well with the number from the input matching rule (○—○) (from Parker, 1978). (b) Sticklebacks: 6 fish in a tank consume *Daphnia* introduced at two ends with an initial profitability ratio of 2:1; after the start of feeding (first arrow) the observed number of fish in patch 2 quickly approaches the number predicted from the input matching rule (indicated by dotted lines). At the second arrow, the patch profitabilities are reversed, and the fish distribution soon approaches the new prediction (from Milinski, 1979). (c) Ducks: in a similar experiment in which 33 ducks were fed pieces of bread from two stations (with profitability ratio of 2:1) around a pond, the number of ducks found at the poorer quickly approaches that predicted by the input matching rule (from Harper, 1982).

Distance between patches  
determines SIZE of territory



**Fig. 11.3.** Although the size of the territories of the golden winged sunbird (*Nectarinia reichenowi*) varies enormously, each territory contains approximately the same number of *Leonotis* flowers (from Gill & Wolf 1975). The energy expended by a sunbird during a day can be determined by time budget analysis (Wolf & Hainsworth 1971, Wolf *et al.* 1975) and this can then be compared with the energy content of the flowers in the territory. The result found is that the number of flowers defended yields just enough nectar to support the sunbird's daily energy requirements.

Golden-winged sunbirds adjust  
territory size to give ~1500 flowers

# Economic Defensibility in Golden-Winged Sunbird 8.3

**Box 5.1** *The economics of territory defence in the golden-winged sunbird (Gill & Wolf 1975).*

(a) The metabolic cost of various activities was measured in the lab:

Foraging for nectar	1000 cal/h
Sitting on a perch	400 cal/h
Territory defence	3000 cal/h



(b) Field studies showed that territorial birds need to spend less time per day collecting enough energy in the form of nectar to survive when the flowers contain more nectar:

Nectar per flower ( $\mu$ l)	Time to get energy (h)
1	8
2	4
3	2.7

(c) By defending a territory a bird excludes other nectar consumers and therefore increases the amount of nectar available in each flower. The bird therefore saves foraging

time because it can satisfy its energy demands more rapidly. It spends the spare time sitting on a perch, which uses less energy than foraging. For example, if defence results in an increase in the nectar level from 2  $\mu$ l to 3  $\mu$ l per flower, the bird saves 1.3 h per day foraging time (from (b)). It therefore saves:

$$\begin{array}{ccc} (1000 \times 1.3) & - & (400 \times 1.3) = 780 \text{ cal} \\ \text{foraging} & & \text{resting} \end{array}$$

       = Benefit of defense

(d) But this saving has to be weighed against the cost of defence. Measurements in the field show that the birds spend about 0.28 h per day on defence. This time could otherwise be spent sitting, so the cost of defence is:

$$(3000 \times 0.28) - (400 \times 0.28) = 728 \text{ cal}$$

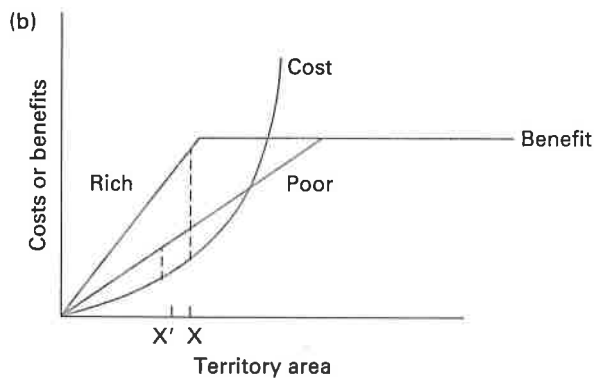
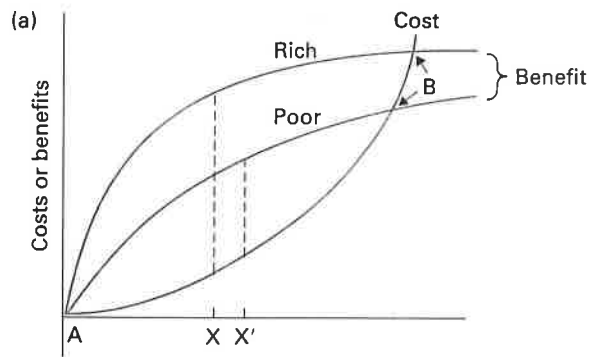
       = Cost of defense

In other words, the flowers are just economically defensible when the nectar levels are raised from 2 to 3  $\mu$ l as a result of defence. Gill and Wolf found that most of their sunbirds were territorial when the flowers were economically defensible.

# Economic Defensibility: Graphical Model

- CONCLUSIONS DEPEND ON SHAPES OF B AND C CURVES
- CAREFUL ABOUT ASSUMPTIONS

8.9



# Adjustment of territory size to energetic optimum : Rufous Hummingbirds.

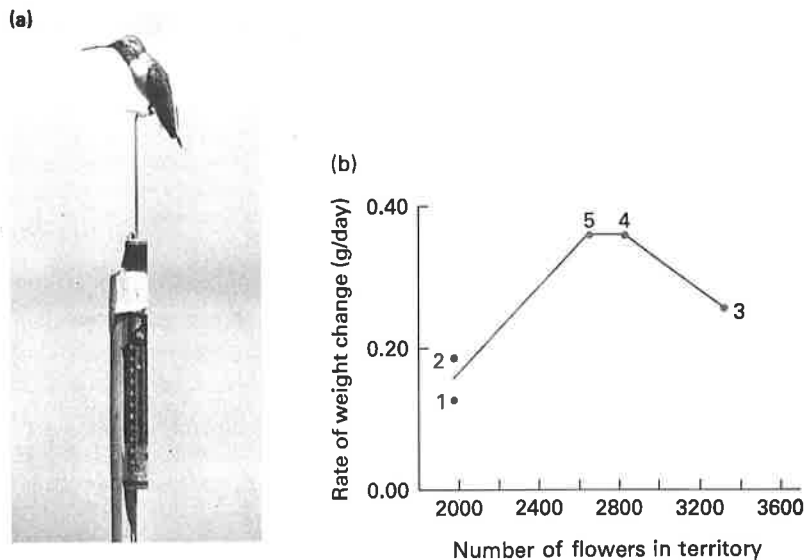


Fig. 5.7 (a) A rufous hummingbird weighing itself by sitting on a perch attached to a balance. Photo by Mark Hixon. (b) The daily weight gain of one territorial bird plotted against its territory size (measured as number of flowers defended) for five successive days. The bird started with a small territory on the first day, enlarged its territory on the third day and then gradually moved towards an intermediate size at which daily weight gain was maximal.

# Economic Defensibility in Honeycreepers.

-  $E + T \leq aP + e(1-a)P$

Basic Cost of living	+	Added Cost of territorial defense		yield if NOT territorial		extra yield due to territorial defense of food
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- territoriality favored when above is true.

$P$  = productivity     $e$  = efficiency of defense

$a$  = % available (of  $P$ ) w/o defense

$P = E + T$      $P = E/a$

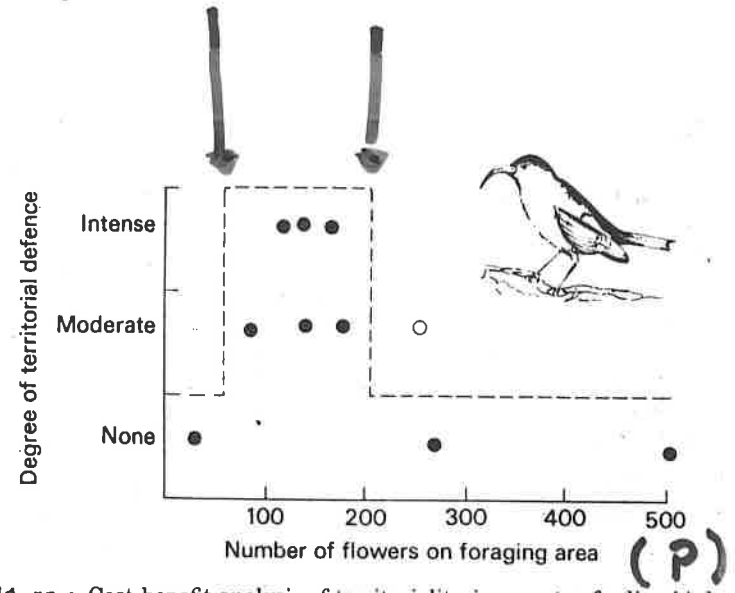


Fig. 11.4. Cost-benefit analysis of territoriality in a nectar-feeding bird, the Hawaiian honeycreeper, *Vestiaria coccinea*. A model, described in the text, predicts that the birds should defend a territory between two threshold levels of resource abundance (dotted lines). Ten birds were observed and their behaviour was classed as intensely-, moderately-, or non-territorial, depending on their degree of defence of the food resources they were exploiting. The behaviour of nine of the ten birds (solid circles) fitted the predictions of the model while one bird (open circle) did not (Carpenter & MacMillen 1976a).