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**FOOD DEMAND FOR COLONY DEVELOPMENT,
CROP PREFERENCE AND FOOD AVAILABILITY FOR
BOMBUS TERRESTRIS (L.) (HYMENOPTERA: APIDAE)**

A thesis

submitted in fulfilment of

the requirements for the degree

of

Doctor of Philosophy

in Zoology

by

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1990

I am tempted to give one more instance showing how plants and animals are bound together by a web of complex relations. I find from experiments that humble-bees (bumble bees) are almost indispensable to the fertilisation of the heartsease (wild pansy) and some kinds of clover. Humble-bees alone visit red clover, as other bees cannot reach the nectar. Hence, we may infer that, if the whole genus of humble-bees became extinct or very rare in England, the heartsease and red clover would become very rare, or wholly disappear. The number of humble-bees in any district depends in a great measure on the number of field-mice, which destroy their combs and nests. Now the number of mice is largely dependent, as everyone knows, on the number of cats; and Col. Newman says 'Near villages and small towns I have found the nest of humble-bees more numerous than elsewhere, which I attribute to the number of cats that destroy the mice.' Hence it is quite credible that the presence of feline animals in large numbers might determine, through the intervention first of mice and then of bees, the frequency of certain flowers in that district!

Charles Darwin 1882.

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ABSTRACT

Eight *Bombus terrestris* (L.) colonies were reared in laboratory observation hives in 1986 and foraged in cages. Pollen and sugar consumption were correlated and could be estimated from larval area and number of live workers. Pollen consumption peaked within two weeks of maximum larval area in 6-8 week old colonies and coincided with peak worker emergence. Sugar consumption peaked with the emergence of males and queens two weeks later. The optimum period for maximum pollination efficiency for a colony would be from one week prior to peak larval area to two weeks after.

There was a positive correlation between the total productivity of a colony ('Productivity Index', a biomass estimate from the number and size of empty cocoons) and the maxima of live worker numbers, larval area and rate of food consumption, and the total food consumption and biomass (but not sex ratio) of reproductives produced. Colonies with higher consumption made greater investment in reproductives, but larger colonies did not invest proportionally more into reproduction than smaller colonies. Larger colonies grew faster with more workers emerging per unit time than smaller colonies.

Food consumption and development of indoor colonies was compared with ten colonies maintained in the same observation hives but free foraging outdoors on flowering crops in 1987. Maximum weekly pollen consumption was 12.6 times less in free foraging colonies and sugar energy consumption was 43 times lower with no queens produced in colonies foraging outdoors. The pollen consumption/cm² at maximum larval area was 14 times lower in free foraging than indoor colonies so consumption (rate and total) for free foraging colonies could not be predicted from maximum larval area using indoor consumption data.

The order of *B. terrestris* nectar gatherers' and queens' crop preference over the whole season was: borage, *Borago officinalis* > fodder radish, *Raphanus sativus* > swede, *Brassica napus* > broccoli, *Brassica oleracea*. Flower preference was not correlated with flower density or production. *B. terrestris* males and honey bees preferred borage with broccoli as second choice. Honey bees were on average seven times more abundant on crops than *B. terrestris* workers and with a similar tongue length honey bees provided the greatest competition for food. On calm, warm days honey bee numbers on borage exceeded 2/m², nectar and pollen became depleted and *B. terrestris* switched to nectar gathering on fodder radish. The long corolla tube of fodder radish excluded nectar collection by honey bees with a short tongue, whereas *B. terrestris* workers bit holes in the corolla base and 'robbed' nectar. Honey bees and *B. terrestris* males removed nectar from previously perforated fodder radish flowers.

Borage secreted nectar throughout the season and had the most pollen and nectar per flower. Fodder radish had the highest flower density and pollen and nectar standing crop, producing nectar later in the season as weather improved. *B. terrestris* being less sensitive to poor weather, foraged for nectar and pollen each day before and after the peak in honey bee numbers.

B. terrestris workers collected pollen on borage by vibrational pollen harvesting ('buzz' pollination) from poricidal-like anthers. On crucifers, incidental dusting of pollen while nectar collecting occurred. Early in the season borage pollen was collected throughout the day, but later in the season with increasing honey bees on borage, *B. terrestris* pollen gatherers collected borage pollen early in the day and crucifer pollen during the rest of the day.

Sugar concentration of nectar returning in foragers was highly correlated with sugar concentration of the most preferred crop at that time. With higher temperature and decreased rainfall, more pollen and nectar became available, more pollen and nectar gatherers and honey bees foraged on the crops and workers returned to colonies with more food. The high density of honey bees on borage did not reduce the food intake returning to *B. terrestris* colonies.

LIST OF ABBREVIATIONS AND SYMBOLS

p or PR	= probability
S.D.	= standard deviation of sample
S.E. (M.)	= standard error of mean
S.E.D.	= standard error of difference
t test or t	= Student's t test
df (DF)	= degrees of freedom
F _s or VR or F ratio	= variance ratio
F. prob. or F PR	= variance ratio probability
n.s.	= not significant ($p > 0.05$)
n	= number of cases (observations)
Reps.	= number of replicates
L.S.D.	= least significant difference (Sokal and Rohlf 1969, p.235)
*	= $p < 0.05$
**	= $p < 0.01$
***	= $p < 0.001$
r value or R	= Pearson's correlation coefficient
z value	= Fisher's transformation for correlation coefficients r
ANOVA	= analysis of variance
temp.	= temperature
R.H.	= relative humidity
μm	= micron (10^{-6} m)
nm	= nanometre (10^{-9} m)
mg	= milligram (10^{-3} g)
μl	= microlitre (10^{-6} litres)
μE	= micro Einstein
kJ	= kilojoule
% sugar	= percentage total sugar content in solution
RSQ or R ²	= R squared (% of variance accounted for by the regression coefficient)
INT	= y intercept
LIN	= linear function (slope)
INT S.E.	= standard error of y intercept
LIN S.E.	= standard error of slope
S.E. REG	= standard error of regression equation
SS	= sum of squares (sum of squared deviations from the mean)
SS %	= percentage sum of squares
MS	= mean square
MV	= missing values
QUAD	= quadratic function
CUB	= cubic function
QUART	= quartic function

COV EF	= covariance efficiency
% VAR	= percentage of variance
CUM %	= cumulative percentage
coef	= coefficient
\pm	= \pm one standard error of mean (figures)
$y=1.3324*x^{0.325}$	= $y=1.3324$ multiplied by $x^{0.325}$ (fig. 3.14)

Note: All levels of statistical significance have been recorded in the appropriate tables or in the appendix and are therefore not generally recorded in the text.

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DECLARATION

This thesis does not contain any information which has been accepted for the award of any other degree or diploma in any University and, to the best of my knowledge and belief, this thesis does not contain any information previously published or written by any other person, except when due reference is made in the text of the thesis.

Consent is given for this thesis to be made available for photocopying and loan.

A handwritten signature in cursive script, reading "D. R. Woodward". The signature is written in black ink and is positioned above the printed name.

D.R. WOODWARD. B.Sc, M.Sc (Hons).

APRIL 1990