Effects of household dynamics on resource consumption and biodiversity

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Human population size and growth rate are often considered important drivers of biodiversity loss[1–6], whereas household dynamics are usually neglected. Aggregate demographic statistics may mask substantial changes in the size and number of households, and their effects on biodiversity. Household dynamics influence per capita consumption[7,8] and thus biodiversity through, for example, consumption of wood for fuel[9], habitat alteration for home building and associated activities[10–12], and greenhouse gas emissions[13]. Here we report that growth in household numbers globally, and particularly in countries with biodiversity hotspots (areas rich in endemic species and threatened by human activities[14]), was more rapid than aggregate population growth between 1985 and 2000. Even when population size declined, the number of households increased substantially. Had the average household size (that is, the number of occupants) remained static, there would have been 155 million fewer households in hotspot countries in 2000. Reduction in average household size alone will add a projected 233 million additional households to hotspot countries during the period 2000–15. Rapid increase in household numbers, often manifested as urban sprawl, and resultant higher per capita resource consumption in smaller households[15–19] pose serious challenges to biodiversity conservation.

As a first step towards quantifying the effects of household dynamics on biodiversity, we compared the rates of change in human population size and the number of households in 76 hotspot and 65 non-hotspot countries. We also investigated the sources of growth in household numbers, comparing the relative contributions of changes in aggregate population size and household size. Finally, in six representative hotspot areas, we estimated the relative contributions of changes in population size and household size to the growth in the number of households (see Methods).

In hotspot countries, the annual rate of growth in the number of households (3.1%) was substantially higher than the population growth rate (1.8%) between 1985 and 2000 (Fig. 1a). Over 80% of
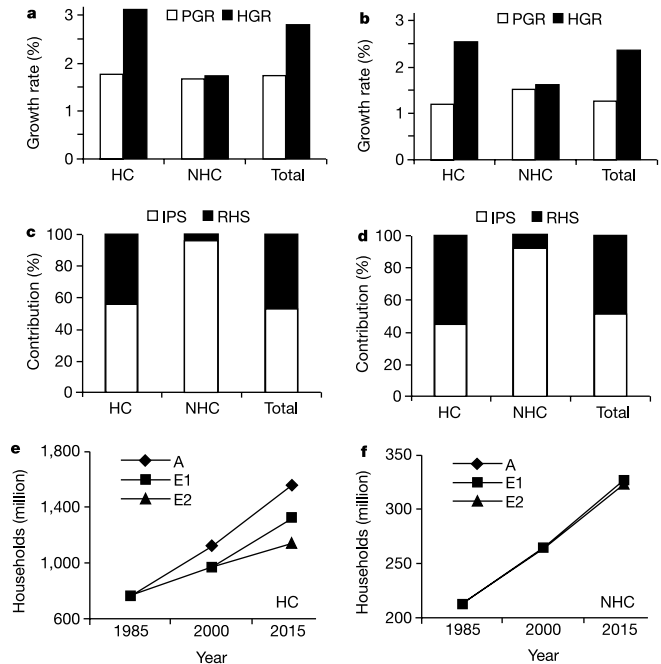
Figure 1 Household dynamics in 76 hotspot countries (HC) and 65 non-hotspot countries (NHC). **a**, Annual growth rates of population size (PGR) and household number (HGR) from 1985–2000. **b**, Projected PGR and HGR from 2000–15. **c**, Contributions of reduction in household size (RHS) and increase in population size (IPS) to household numbers during 1985–2000. **d**, Projected contributions of RHS and IPS from 2000–15. In **e** (HC) and **f** (NHC), 'A' indicates the actual household number; E1 is the estimated household number assuming that the average household size in 2000 was at the 1985 level and that the average household size in 2015 remains at the level in 2000; E2 assumes that average household sizes in both 2015 and 2000 were at the 1985 level.

hotspot countries showed this pattern (Table 1). In contrast, population and household growth rates in non-hotspot countries were roughly equivalent (1.7%) (Fig. 1a). The divergence in population and household growth rates is expected to become more pronounced over the next 15 years (Fig. 1b and Table 1), suggesting that it is crucial to consider growth in the number of households when assessing threats to biodiversity.

The growth in household number resulted directly from a simultaneous increase in population size and reduction in average household size. In 1985, average household size was larger by 1.0 persons in hotspot countries (4.7) than in non-hotspot countries (3.7). This difference was reduced to 0.3 persons in 2000. By 2015,

Table 1 Comparisons between rates of growth in household number and population size in 76 hotspot and 65 non-hotspot countries

Time period (years)	Relationship between *hhn* and *pop*	Hotspot countries		Non-hotspot countries		Total	
		Number of countries	Per cent	Number of countries	Per cent	Number of countries	Per cent
1985–2000	$hhn(+) > pop(+)$*	63	82.9	42	64.6	105	74.5
	$hhn(+) < pop(+)$‖A	11	14.5	19	29.2	30	21.3
	$hhn(+)$ & $pop(-)$‡	1	1.3	3	4.6	4	2.8
	$hhn(-)$ & $pop(+)$§	1	1.3	1	1.6	2	1.4
2000–15	$hhn(+) > pop(+)$	67	88.2	46	70.8	113	80.1
	$hhn(+) < pop(+)$	5	6.6	12	18.5	17	12.1
	$hhn(+)$ & $pop(-)$	4	5.2	6	9.2	10	7.1
	$hhn(-)$ & $pop(+)$	0	0.0	1	1.5	1	0.7

Abbreviations: *hhn*, rate of growth in household number; *pop*, rate of growth in population size. The frequency of hotspot and non-hotspot countries occurring in the categories $hhn(+) > pop(+)$ and $hhn(+) < pop(+)$ differed at $P = 0.0365$ for 1985–2000 and $P = 0.0341$ for 2000–15.
*Both *hhn* and *pop* are positive, and the former is greater than the latter.
†Both *hhn* and *pop* are positive and the former is smaller than the latter.
‡*hhn* is positive whereas *pop* is negative.
§*hhn* is negative whereas *pop* is positive.

the average household size in hotspot countries (3.4) is expected to be 0.2 persons smaller than that of non-hotspot countries (3.6). Per cent contribution of reduced household size to growth in the number of households was about 12 times higher in hotspot countries than in non-hotspot countries in 1985–2000 (Fig. 1c), and it is estimated to be about 7 times higher in hotspot countries than in non-hotspot countries in the period 2000–15 (Fig. 1d). Furthermore, this contribution is projected to increase from 43% (hotspot countries) and 3% (non-hotspot countries) in 1985–2000 (Fig. 1c) to 54% and 7%, respectively, in 2000–15 (Fig. 1d). Most countries containing hotspots have relatively low population growth rates, and the primary demographic pressure on their biodiversity will come from urban sprawl and other impacts associated with increased household numbers.

Had the average household size remained at the 1985 level, there would have been 155 million fewer households in hotspot countries in 2000 (Fig. 1e). By 2015, 233 million more households are likely to be added to hotspot countries as a result of continued reduction in average household size alone. If the average household size in 2015 were the same as in 1985, there would be 415 million fewer households in hotspot countries (Fig. 1e); in non-hotspot countries, there would be 4 and 7 million fewer households in 2000 and 2015, respectively (Fig. 1f). In four hotspot countries (Italy, Portugal, Spain and Greece) over the period 2000–15, contributions of reduction in average household size to growth in the number of households are expected to be roughly 120–190% (equivalent to 0.4–2.4 million additional households in each country) even when their corresponding population sizes are projected to decline at an annual rate of 0.1–0.3%.

In the six representative hotspot areas listed in Table 2, reduction in average household size contributed approximately 30–73% to the growth in the number of households over the periods of 10 and 40 years. Annual rates of population growth in these six areas ranged from 0.5% to 7.0%, whereas annual rates of growth in household numbers were much higher (1.7–10.0%) owing to a decline in average household size (0.7–1.2% per year). By 1991, Italy had added almost 6 million households as a result of reduced average household size alone since 1951 (Table 2). In Brazil, over 4.6 million
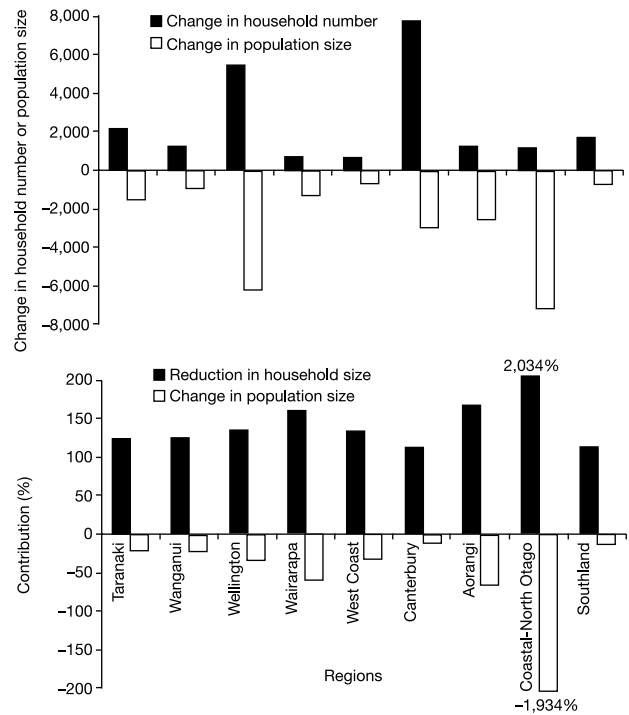

Figure 2 Changes in household numbers and population size (top) as well as their contributions to growth in household number (bottom) in nine regions of New Zealand.

households were created between 1991 and 2000 owing to a reduction in average household size. Had the average household size stayed at the 1970 level, Indian River County (United States) would have had 11,103 fewer households in 2000. These extra households are among the factors that have made Indian River County one of the endangered species hotspots in the United States (areas with the largest numbers of federally listed endangered and

Table 2 **Dynamics of human populations and households in six biodiversity hotspot areas**

	New Zealand	Italy	Brazil	Indian River County, USA	Island of Rodrigues, Mauritius	Wolong Nature Reserve, China
Relationship with biodiversity hotspots	Is identical to 'New Zealand'	Contains a portion of 'Mediterranean Basin'	Contains a portion of 'Brazilian Cerrado' and 'Atlantic Forest Region'	Contains a portion of 'Caribbean'	Is part of 'Madagascar and Indian Ocean Islands'	Is part of 'Mountains of South-Central China'
Time period						
T_0	1976	1951	1991	1970	1983	1975
T_1	1991	1991	2000	2000	2000	1998
Population size						
T_0	2,975,846	47,516,000	145,605,330	35,743	32,925	2,560
T_1	3,237,915	56,322,185	168,370,893	110,558	35,769	4,320
Average annual growth rate of population size (%)	0.6	0.5	1.7	7.0	0.5	3.0
Average household size						
T_0	3.22	4.02	4.95	2.90	4.95	6.08
T_1	2.75	2.83	3.76	2.25	4.13	4.95
Average annual rate of growth of household size (%)	−1.0	−0.7	−1.2	−0.8	−1.0	−1.1
Number of households						
T_0	923,257	11,814,402	34,734,715	12,325	6,652	421
T_1	1,177,665	19,909,003	44,795,101	49,137	8,651	942
Average annual rate of growth in the number of households (%)	1.8	1.7	3.2	10.0	1.8	5.4
Extra number of households due to reduction in average household size	172,101	5,905,027	4,629,573	11,103	1,424	231
Contribution of reduction in average household size to growth in number of households (%)*	67.7	73.0	46.0	30.0	71.3	44.4

*The remainder of the contribution came from population growth.

threatened species)[20]. Reduction in average household size was an important factor causing the increase of household number and thus rise in the amount of fuel wood consumed in Wolong Nature Reserve (China), which contributed to increased deforestation and loss and fragmentation of habitat for giant pandas[21]. In Wolong, there would have been approximately 230 fewer households in 1998 if average household size had been kept at the 1975 level (Table 2).

Even in regions where population size decreased, the number of households still increased substantially owing to a reduction in average household size. During the period 1976–81, population size in nine government regions of New Zealand declined by about 640–7,200 people, but the number of households rose by approximately 560–7,650 per region (Fig. 2, top). Contributions of reduction in average household size to the increase in the number of households ranged from roughly 112–2,034%, compared with −1,934% to −12% resulting from the change in population size (Fig. 2, bottom). In the other 13 regions of New Zealand where the population increased, reduction in average household size contributed about 29–82% to the growth in the number of households, whereas population growth accounted for approximately 18–71%. Considering all 22 New Zealand government regions, contributions of reduction in average household size and change in population size to growth in household number were about 83% and 17%, respectively.

Reduction in average household size takes a double toll on resource use and biodiversity. First, more households mean more housing units, thus generally increasing the amount of land and materials (for example, wood, concrete and steel) needed for housing construction (see Supplementary Results). Second, smaller households have lower efficiency of resource use per capita (Fig. 3) because goods and services are shared by more people in larger households[16–18] (see Supplementary Results). Proximate causes of a reduction in household size include lower fertility rates, higher per capita income, higher divorce rates, ageing populations, and a decline in the frequency of multi-generational families living together (see refs 22–24). Some of these factors can affect both population growth and household growth. Although lower fertility rates may reduce population growth and household numbers, the resulting potential reduction in resource consumption may be off-set by higher per capita consumption in smaller households. Thus, declining fertility rates are necessary but not sufficient to ensure reduced anthropogenic pressure on the environment and natural landscapes. Our study suggests that biodiversity conservation is faced with much larger challenges than previously thought, because reduction in household size leads to higher per capita resource consumption and a rapid increase in the number of households, even when population size declines. This trend is most prevalent in hotspot countries where it may severely limit efforts to conserve biodiversity, thus degrading the ecosystem services[25] that biodiversity delivers to humanity. □
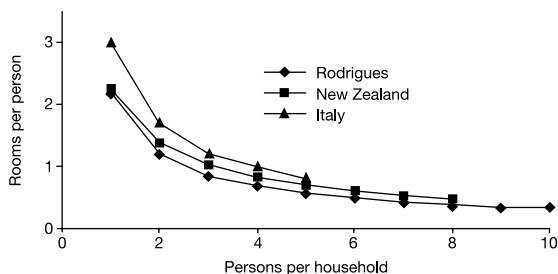
Figure 3 Rooms per capita versus household size in New Zealand, Italy and Rodrigues of Mauritius.

Methods

Data on population sizes and household numbers for 141 countries over the period 1985–2015 are from the United Nations[26]. The hotspot countries were identified according to Conservation International (http://www.biodiversityhotspots.org/xp/Hotspots/) and ref. 27, confirmed by N. Myers and P. Langhammer (personal communication), and are listed in Supplementary Table 1. The six areas used in our detailed analysis were chosen from six major regions (Africa, Asia, Europe, North America, Oceania and South America) on the basis of data availability, representation and policy implications (see Supplementary Methods).

Rates of growth and per cent contributions in hotspot and non-hotspot countries (Fig. 1) were weighted by population size and number of households in each country because of great variations among countries. To compare the rates of growth in household number (hhn) and population size (pop) (Table 1), we determined the number and percentage of hotspot and non-hotspot countries with $hhn(+) > pop(+)$ and $hhn(+) < pop(+)$ (where + indicates positive rates of growth). Using Fisher's exact test, we tested for differences in the frequency of occurrence of hotspot and non-hotspot countries in these categories, for 1985–2000 and 2000–15, respectively.

Changes in the number of households are affected directly by changes in population size and household size. We calculated the per cent contribution of change in average household size (chs) to the change in the number of households (H_{chs}) as the total contribution (100%) minus the contribution due to population growth alone:

$$H_{chs} = [H_1 - H_0 - H_P]/[H_1 - H_0] \times 100\% = 100\% - H_P/[H_1 - H_0] \times 100\% \quad (1)$$

where H_0 and H_1 are the number of households at time 0 and 1, respectively. H_P is the growth in the number of households (with the same average household size at time 0 (S_0)) due to population growth or the difference in populations ($P_1 - P_0$) at times 1 and 0: $H_P = (P_1 - P_0)/S_0$. The average household size was fixed at its value for time 0 (S_0) (when H_P was computed) to see how many fewer households would exist at time 1 if the average household size remained static. As in standard decomposition techniques[28], taking a simple average of household sizes at times 0 and 1 would be another way to calculate H_P. However, our choice of S_0 yields similar results and is the most appropriate method to address our question.

The contribution of change in population size (cps) to growth in the number of households (H_{cps}) is the total contribution minus the contribution owing to change in household size:

$$H_{cps} = 100\% - H_{chs} = 100\% - (100\% - H_P/[H_1 - H_0] \times 100\%)$$

$$= H_P/[H_1 - H_0] \times 100\% \quad (2)$$

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The genetic basis of family conflict resolution in mice

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Asymmetries in the costs and benefits of parental investment for mothers, fathers and offspring result in family conflict over the production and provisioning of young[1–3]. In species where females provide most resources before and after birth, the resolution of this conflict may be influenced by genes expressed in mothers and by maternally and paternally inherited genes expressed in offspring[4,5]. Here we disentangle these effects by means of reciprocal mating and cross-fostering of litters between two strains of mice that differ with respect to the typical resolution of family conflict. We find that differences in litter size between these two strains are determined by paternal genotype, whereas differences in provisioning are under maternal control, showing that there is antagonistic coadaptation of maternal and paternal effects on distinct life-history traits. Maternal provisioning is also influenced by the type of foster offspring. Contradictory to theoretical expectations, however, we find no evidence for a negative correlation across strains between maternal provisioning and offspring demand. Instead, we show that there is positive coadaptation such that offspring obtain more resources from foster mothers of the same strain as their natural mother, irrespective of their father's strain.

Offspring are typically selected to demand more resources from parents than parents are selected to provide[1,2,6]. In addition to this parent–offspring conflict over provisioning, conflicts will often arise between mothers and fathers[7,8]. Each parent favours greater investment by the other than is in the other's best interest[9]. Even where males provide little or no direct care, this sexual conflict can manifest itself in parent-of-origin-specific effects on solicitation

behaviour in offspring that affect resource transfer from mothers, for example, through genomic imprinting[5,10,11]. Biologists have begun to investigate the genetic basis of these family conflicts and their resolution; previous studies have focused either on sexual conflict between paternally and maternally inherited genes[10], or on coadaptation of maternal and offspring genes[4,12]. Here we report the results of a study that has assessed simultaneously the influence on maternal investment of genes expressed in mothers, and maternally and paternally inherited genes expressed in offspring.

We conducted a series of crosses using mice of two strains, CBA and C57/B6 (hereafter called B6), that differ in the resolution of family conflict. CBA litters typically contain more pups than B6 litters (Fig. 1), but the individual birth weight of CBA pups is typically less than that of B6 pups (Fig. 2). To determine the contribution of maternal genes and of maternally and paternally inherited offspring genes to differences between the strains in maternal investment, we carried out crosses that included pure strain CBA matings, pure strain B6 matings, and both possible reciprocal crosses (male CBA with female B6, and female CBA with male B6). The resulting 117 litters were all cross-fostered among (unrelated) females, yielding foster families that included all eight possible combinations of foster mother's strain, natural mother's strain and father's strain.

We recorded the size of each litter and measured maternal provisioning 6 d after birth, a stage at which pups gain weight only by suckling. After simulated departure of the foster mother for
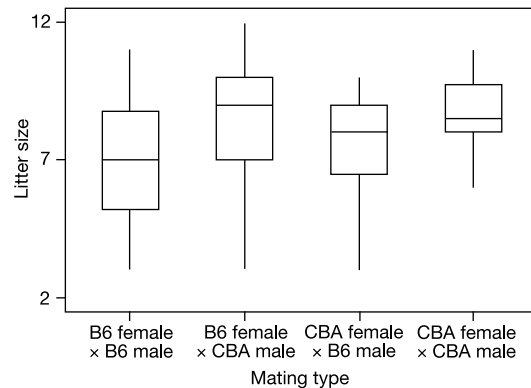
Figure 1 Litter sizes produced by all four possible types of mating (B6 female × B6 male, B6 female × CBA male, CBA female × B6 male and CBA female × CBA male).
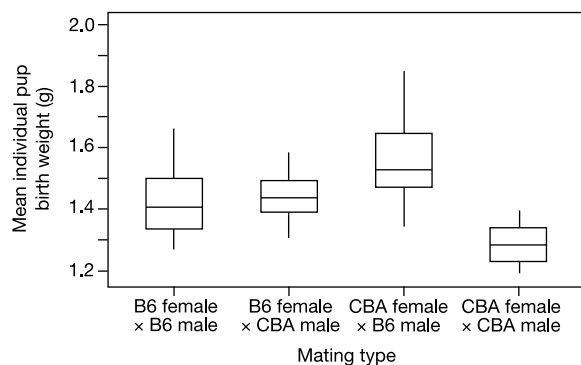
Figure 2 Mean individual birth weight of pups in litters produced by all four possible types of mating (B6 female × B6 male, B6 female × CBA male, CBA female × B6 male and CBA female × CBA male). Note that each litter contributes a single mean value of pup birth weight to the data set.

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