The role of local adaptation in sustainable village chicken production

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Key words: local adaptation, management intervention, village chickens, phenotypic diversity, genomic variation, disease resistance

Abstract

Village chickens are ubiquitous in smallholder farming systems, contributing to household,

local and national economies under diverse environmental, economic and cultural settings. However, they are raised in challenging environments where productivity is low while mortality is high. There is much interest in utilizing indigenous genetic resources to produce a chicken resilient to its environment, whilst providing the basis of an economically sustainable enterprise. Globally, however, a wide variety of interventions have so far proved unable to deliver sustainable improvements. Here, we show that regional differences in trait preferences and parasite burden are associated with distinct chicken genepools, likely in response to interacting natural and human-driven (economic and social) selection pressures. Drivers of regional differences include marketing opportunities, cultural preferences, agro-ecologies and parasite populations, and are evident in system adaptations, such as management practices, population dynamics and bird genotypes. Our results provide sound multidisciplinary evidence to support previous observations that sustainable poultry development interventions for smallholder farmers, including breeding programs, should be locally tailored and designed for flexible implementation.

Main

For millions of smallholders in the least developed countries livestock are vital components of their livelihoods, contributing to economic, nutritional and social well-being, and improving families' resilience as an asset that can be sold in times of need[1]. Indigenous chickens are of especial value to women and children[2] and improving production has become widely accepted as a viable strategy towards poverty alleviation[1,3], and increasing household food security[4]. In this paper, we examine the village production system as a whole and, by comparing two contrasting regions in Ethiopia as cases studies, illustrate how unique adaptations to local circumstances have implications for the success of any widespread

intervention program. In doing so, we highlight barriers impeding the transformations required to achieve more sustainable increases in chicken production and, consequently, improvements to local economies, livelihoods and nutrition.

Whilst village chickens are widely accessible and require few inputs, productivity is low and constrained by, among other things, disease, predation and scarcity of feed[5]. Interventions to improve production include vaccination[4,6]; bird distribution[7]; management interventions[8]; cross-breeding programs[9]; and combined programs[10], but few interventions have been demonstrably sustainable in village chicken production systems[8,11]. In Ethiopia, where indigenous birds still account for over 97% of egg and meat production[12], government-led programs for village poultry development through genetic improvement have included a cockerel exchange program and distribution of high-producing exotic birds[13] combined with farmer training on poultry management, based on a commercial model with larger flock sizes and increased inputs[14]. However, in rural areas, exotic birds adapted poorly to a scavenging environment and were reported by farmers to negatively impact the local birds' brooding and scavenging abilities[15], and may also have introduced very virulent Infectious Bursal Disease virus into indigenous chicken populations[16]. One alternative to exotic gene introgression is to selectively breed indigenous ecotypes to produce birds that are productive under village conditions while retaining locally-acceptable morphological and adaptive traits[17].

Globally, the conventional top-down transfer of technology from researchers to farmers has been criticized for often being inappropriate to the social, physical and economic settings in which farmers operate[18]. Sustainable agriculture and development implies that systems should avoid the over-exploitation of natural resources, whilst providing for the existing and

emerging economic and basic food needs of families and communities[19]. System changes

impact on the future availability of resources, and therefore agro-ecologies need to remain

resilient to ensure they can continue to support future generations. Resilience is dependent

on adaptability and one approach is to investigate the system using three "pillars" of

sustainability, namely environmental, economic and social[20].

The aims of our unique, large-scale multidisciplinary study were, therefore, to map the

contexts of local chicken production systems, together with investigation of indigenous

chicken genetics and health, to identify the challenges facing sustainable productivity

increases in this system. Using two Ethiopian indigenous chicken ecotypes for detailed case

studies, we employed a systems approach to study the climatic, social, cultural, economic,

market, bird productivity and production characteristics, as well as infection prevalence in

two distinct geographic woredas (local administrative districts; Horro and Jarso) of Ethiopia

(Fig. 1, Table 1, Supplementary Fig.1, Supplementary Table 1) in parallel with genomic

studies of adaptive traits in the chickens themselves. We identify key selection pressures

that impact on the sustainability and resilience of village chicken production, and suggest

how poultry development programs globally could address constraints whilst building on the

existing strengths of the local poultry production systems.

Results and Discussion

Bird and system adaptations to the cultural and economic environment

More than 70% of the households in the study regions owned chickens (Table 1), with

production, and income from sales, often managed by women. Using the FAO classification

system[3], households in the study engaged in 'small scale extensive scavenging' (1-5 adult

chickens, rarely keep other livestock, often landless) or 'extensive scavenging' (5-50 adult chickens, usually keep other livestock) chicken production. However, strict classification using this system was problematic; although two-thirds of all participants (66%; 267/400) kept 1-5 adult chickens (Horro 58%, 115/200; Jarso 76%, 152/200; P<0.001), only 9 (3 from Horro, 6 from Jarso) kept no other livestock. Although demographic characteristics, such as family size, proportion of female-headed households and age of household heads were broadly similar between the two woredas, there was significant variation in education, agricultural production and land ownership. Furthermore, chicken flocks were larger and more valuable in Horro (Table 1), mostly due to the greater numbers of young stock. Flock size also increased with household income, as did the number of birds consumed and sold (Fig. 2).

Consumption and sale of chickens and eggs were low, particularly in Jarso where both were significantly lower than in Horro (Table 1), and this is likely to have impacted development of market-oriented food systems, which halts if there is limited demand for farmers' products[21]. Furthermore, the roles for chickens differed between the communities; Horro farmers were more likely to sell chickens (around twice as many) where the average prices received for both hens and roosters were significantly higher in Horro ($P < 0.001$ for both). Neverthless, the median income from sale of chickens was low, despite reportedly being an important source of additional income for incidental expenses in Horro. Chicken production offered even less income in Jarso, where sale of khat provided an important alternative source of incidental or continuous income. Whilst income from chicken production tended to contribute a greater proportion of family income in poorer households, a smaller proportion of the poorest families derived income from their chickens compared to wealthier

households (Fig. 3; Chi-square for trend 10.7, P = 0.001).

In Horro, 70% of farmers reported that the purpose of egg production was hatching; just 8.5% reported that they had sold eggs in the past year, compared to 18.5% in Jarso. The greater emphasis on sale and consumption of chickens in Horro may have driven this preference for using eggs for rearing replacement birds. This is consistent with the larger populations of young stock with greater infection-susceptibility and greater fluctuation in chicken population numbers observed in Horro, factors relevant for sustained transmission of infectious organisms.

Markets are also influential in dictating the characteristics of the local chickens[17]. Village chickens are often assumed by outside researchers to mate in an uncontrolled manner[22], but farmers actually select their breeding stock based on morphological traits[23]. For example, the greater marketing opportunities in Horro, compared to Jarso, may have resulted in greater human-driven selection pressure in favor of the rose comb variant and higher body weight; the rose comb has strong cultural significance and increases the market value of roosters in Ethiopia and was observed in higher frequency in Horro[22]. Our genome wide association study (GWAS) for rose versus simple comb identified a strong signal of selection in the genomic region previously associated with the rose comb phenotype[24] in the Horro chickens (Supplementary Fig. 2C and Supplementary Table 2), confirming results from our previous studies[22]. Indeed, human selection for rose comb must have been particularly strong given that homozygotes for this mutation have lower sperm mobility[24]. Our previous studies also identified a stronger signal of selection in the Horro chickens in the genomic regions associated with body weight[25], probably a result of the greater importance attached to body size in Horro (reported as important by 43% of respondents in Horro vs 12% in Jarso), and

reflected in the greater weight of males and females of the same age in Horro compared to Jarso ($P < 0.01$; see[26]). The predicted weight for a 6-month-old male bird in Horro was 1.65 kg; almost 20% greater than for an equivalent bird in Jarso (1.38 kg).

In summary, the role of chickens and demand for products between regions (e.g. sale and consumption) is associated with variation in flock (size, age distribution) and bird phenotypic (weight, rose comb) and genomic characteristics.

Bird and system adaptations to the natural environment

The major constraints to livestock production reported by farmers varied between the woredas, with disease and shortage of land most important in Horro and Jarso, respectively; the median land holding size in Horro was approximately 5 times larger than in Jarso (Table 1). This difference was also reflected in the size of the livestock holdings (in terms of Tropical Livestock Units; TLU[27]). Scarcity of feed and water, predation and inadequate veterinary and extension services were noted as major chicken production constraints in both woredas.

Our genomic studies show compelling evidence of co-adaptation of these two chicken populations with their parasite populations; parasitic infections were more prevalent and less aggregated in the Horro population compared to Jarso (Supplementary Note 1). Macroparasites tend to cause density-dependent pathology; hence, both the number of chickens infected (prevalence) and the distribution of macroparasites among hosts (aggregation) matters.

GWAS analyses indicated that genetic resistance to both ascarids and lice parasitism are heritable complex traits. However, distinct genomic regions are associated with these traits in the two populations (Fig. 4, Supplementary Note 2 and Supplementary Table 3). In the

Horro chickens, genome-wide significant associations were identified on chromosomes 1 (P = 9.16E-08) and 4 (P = 9.86E-10) for ascarids, and on chromosomes 1 (P = 8.75E-09) and Z (P = 1.10E-07) for lice resistance. In Jarso chickens, two genome-wide significant associations were identified for ascarids on chromosome 1 *(P = 1.13E-07 and 1.18E-07)*, albeit 50 Mb and 160 Mb away from the one identified in Horro, respectively. Several other SNP markers that exceeded the suggestive significance threshold were identified for both ascarids and lice resistance in the two populations (Supplementary Table 3). Collectively, the SNP markers associated with parasitic resistance in Horro chickens accounted for more of the phenotypic variance compared to Jarso chickens. This could have been due to lower selective pressures in Jarso compared to Horro or may have arisen if the two traits have different levels of polygenic complexity in the two populations. Although factors other than host genetic difference may also contribute to variation in parasite measurements[28] and thus may reduce the power of a field study compared to controlled challenge experiments, crucially host genetic differences in resistance may still be detected[29,30]. Hence, while the data presented here cannot dissect the direct role of the parasites driving selection for resistance, we provide, for the first time in indigenous village chicken ecotypes, evidence suggestive of co-adaptation with their parasite populations, as evidenced by our signature of selection and GWAS results.

Whilst birds may be adapted to meet farmers' requirements and the local environment, farmers also adapt their management systems accordingly. For example, most Jarso farmers chose to rear chicks during the rainy season, when vegetation affords chicks with protection from predators. In contrast, Horro farmers reported considerably greater numbers of birds lost to disease, prompting farmers to hatch larger numbers of eggs in the lower disease-risk

dry season. This lead to regional and temporal/seasonal variation in flock sizes (see Supplementary Table 4). In Horro, flock size was significantly larger in May/June (pre- main rainy season; median = 11 birds), compared to October/November early dry season; (median = 6 birds), whereas in Jarso the pattern was reversed and the seasonal difference in flock size was lower.

The results of our ecological niche modelling, which highlight considerable bioclimatic dissimilarity between the study woredas (Fig. 1 and Supplementary Figure 1) are consistent with these divergent management strategies being, at least in part, a response to distinct climatic conditions, particularly precipitation, which is an important factor in parasite survival and aggregation. Whilst we might expect that reproductive management of birds by the farmers would be the main driver of flock size, it is notable that greater fluctuations were observed in the poultry population with the higher parasite burden, as is observed in wild game bird populations[31]. The system adaptation to annual population crashes means more chickens can be produced to meet increased demands during the important festivals of Easter and Christmas, but also allows for the regular depopulation in unfavorable conditions, such as in response to, or anticipation of, high epidemic risk during the wet season. However, to allow birds to meet the farmers' annual breeding requirements, which may not coincide with fluctuations in parasite numbers over longer time periods, chickens, particularly in Horro, may be under increased selection for parasite resistance and/or tolerance due to both the social and physical environments.

Implications and recommendations for breeding programs

A major obstacle for a successful breeding improvement intervention in rural areas is the

high level of social and ecological diversity, which makes the identification of suitable breeding goals a difficult task. Our selective sweep analyses, together with our previous findings[25], demonstrate that the genomes of the two chicken ecotypes are distinctly selected (Supplementary Fig. 4; see also Supplementary Note 2 and Supplementary Note 3). SweeD analysis, a likelihood based detection method of selective sweeps based on allele frequencies[32], mapped a total of 51 genomic regions across the autosomal genome (GGA1–28) in both populations that had been subject to positive selection pressure, of which only 7 (13.7%) were common to both populations (Supplementary Fig. 5A). Moreover, calculation of integrated haplotype score statistics (iHS) at the intra-population level revealed 96 regions under selection pressure in Horro chickens, but only 31 in the Jarso population, with only 2 regions in common (Supplementary Fig. 5B). These results are consistent with the hypothesis that indigenous chickens from different geographic regions have developed distinct adaptive mechanisms responding to local selection pressures. This needs to be considered when designing breeding programs. We previously reported the lack of significant genetic correlations between infections and production traits in these populations, suggesting that selection for enhanced host defense against parasitism and viral and bacterial infection may not compromise productivity and *vice versa*[25]. Thus, balanced selection goals towards the enhancement of both productivity and health traits seem to present a valid means for the improvement of indigenous village chickens. However, trade-offs between infection tolerance (i.e. the ability of the host to withstand the pathological consequences of infection) and resistance (i.e. the ability of the host to control pathogen invasion or replication) may complicate the definition of clear goals in breeding programs aiming to improve chicken health. A breeding program aiming to increase

tolerance is much easier to implement without the need of specialized phenotyping. However,

in spatially segregated populations (as our results demonstrate village chickens to be)

tolerance to infection will tend to maintain or increase local pathogen prevalence, whereas

resistance will reduce prevalence[33]. Therefore, determining the relative advantages of

tolerance *versus* resistance as a goal in a localized genetic improvement program may

depend on the environment, economics farmers' preference and attitudes toward investing

in supportive measures, such as complementary infection control. However, to fully realize

the benefit of a breeding intervention, the complex interactions between host population

dynamics, genetic variation and the effects of parasites on host fecundity and mortality need

to be well understood within local agro-ecological and socio-cultural environments, in order

that these may be predicted and mitigated. For example, potentially adverse consequences

of production changes to increase the number of chicks (which tend to be more susceptible

to infection) reared at one time may include altered population susceptibility to, and/or

transmission dynamics of, infection. As mitigation may entail additional costs and

infrastructure (which may not be locally available), the economic and other implications of

system perturbations resulting from interventions also need to be considered, as do the

effects on farmers who are either unable or unwilling to invest in genetically improved birds,

and whose flocks may potentially be put at increased risk by infection-tolerant birds

supporting increased pathogen circulation.

Implications and recommendations for development programs utilizing poultry

The opportunities and choice to move towards increased chicken production will vary greatly

between individual farmers, and will depend on their individual situation and locality. Our

results highlight important social and environmental differences between regions that may

drive the need for different technologies to support increased production that should be

taken into account within intervention planning. As summarise in Fig. 5, sustainable chicken

production interventions need to identify an appropriate balance between inputs (such as

supplementary feed, veterinary measures to prevent and control disease, improved housing,

hatching or brooding facilities, enhanced genetic resource) and outputs (such as increased

growth rates, body weights, egg numbers) and recognise that different farmers may prefer

different trajectories of change, depending on individual-level factors (e.g. attitudes to risk,

desired livelihood role for chicken production) and region-level factors (e.g. access to

markets and services, environmental risks, cultural norms).

In our study, Horro farmers expressed considerable interest in vaccines and are likely to be

receptive to effective disease control programs, particularly against Newcastle disease,

which have already demonstrated economic and social benefits in projects conducted in a

number of developing countries[4,6]. Thus, for a relatively modest investment, Horro farmers

may be able to realize the economic benefits of vaccination (Fig. 5: Trajectory I), provided

they can access stable markets[34]. The same intervention programs may be less readily

received in Jarso, where chickens have lower cultural and economic importance and where

there is poor transport infrastructure, limited local market access and feed shortages. Thus,

a prerequisite for successful up-scaling of poultry production in such regions will be the

connection of farmers to stable markets, without which any investment may carry more risk

than its equivalent in Horro due to the likely lower output for a given level of input. Where

markets exist, greater increases in inputs, moving the farmer toward a semi-intensified

production system, may enable greater output but may also increase risk (Fig. 5: Trajectory

II). Alternatively, a breeding program could make available fertile eggs or young chicks, which farmers can either buy or contract rear, timed for sale during periods of peak demand. This may allow them to depopulate over the rainy season, which would minimize the losses to disease and decrease the supplementary feed requirements, thereby increasing efficiency (Fig. 5: Trajectory III).

However, the low current rate of chicken sale means that interventions to improve production, such as the introduction of improved birds, are unlikely to translate into substantial increase in income for many farmers under the current production systems, especially in Jarso. Furthermore, the observed correlation between wealth, flock size and utilization (both sale and consumption), which has also been noted in other studies[35,36], and the relatively small proportion of the poorest people who participated in chicken sales, would suggest that this latter sector may not achieve the same benefit from interventions as more affluent farmers.

The low level of consumption in both woredas, but particularly Jarso, suggests that the potential nutritional benefits of poultry meat and eggs are not being realized. Alimentary habits, which may be subject to social taboos[4], have been slow to change following previous successful poultry development projects[4]. Hence, successful nutritional impact from poultry development schemes will require further work, sensitive to possible variation between regions, to understand how an increase in production of these valuable sources of protein and micronutrients[37,38] may be better incorporated into local diets.

Given the low use of chickens for sale and consumption, the primary role of chickens in poorer, more precarious, households is likely to be to provide a buffer from shocks and stresses in the subsistence agriculture system[39]. Therefore, in the short term, for such

farmers it may be more important to reduce wastage and the risk of loss than to increase productivity for this sector, particularly as many smallholders believe additional inputs to chicken production would not be profitable[40]. Whilst selective breeding for enhanced resistance to specific key viral, bacterial and parasitic disease[25] has the potential to bring benefits to farmers willing to adapt their production systems, it will necessarily require the adoption of new technologies, with associated additional costs.

Supporting recommendations from fieldworkers[3,5] this study demonstrates that, as well as developing different strains of chickens appropriate to different localities, other flexibilities need to be built in to the program delivery, such as allowing (and assisting) farmers to determine their own capacity to support flocks of varying size, rather than dictating the number of chicks provided, as feed provision is a limiting factor for many farmers. However, the present analysis focused on the household level; given the important role of chicken production to women[41] future studies explicitly examining specific gender aspects are warranted.

Conclusions

Using a combination of clinical, socio-economic and genomic studies, data provided by local communities and agricultural officers, and publicly available census, survey and bioclimatic data, we have established a detailed map of the chicken production systems in two diverse regions of Ethiopia. These data identified two distinct production systems and populations, with indigenous poultry adapted to not only the physical but also the economic and cultural environments. Our results reveal that the apparent ubiquity of chickens in village settings globally is obscuring the underlying divergence which is a consequence of distinct local

adaptations that underpin sustainable chicken production in ecologically, culturally and economically diverse settings; we find that this diversity matters and should be considered in intervention programs.

Globally, poultry development programs need to consider how they can achieve the required flexibility to deliver interventions sustainably[42] and to meet the requirements of "people in places"[43]. Many previous programs have operated according to prescriptive protocols, such as delivering a fixed number of pullets and cockerels according to an "ideal" ratio and requiring farmers to commit to investing additional time and resources into their poultry. Although this may be efficient in terms of program delivery, and allow these programs to claim success in terms of numbers of smallholders reached, in reality, rigid protocols achieve success only where they can be adapted and redefined to meet the primary goals of all actors in the process[44]. Drawing on recommendations from fieldworkers[3,5], we conclude that enabling farmers to exercise greater flexibility in the development and implementation of future improvement programs in terms of the type of chicken used, how breeding strategies are implemented, the numbers of birds kept and the amount and type of inputs required may promote more widespread and sustainable adoption among those groups in society who are most dependent on this valuable resource.

Materials and methods

The study areas

This study was conducted in two geographically distinct woredas (local administrative districts) within the Oromia region in Ethiopia; Horro and Jarso. Oromia is the largest administrative region in the country and includes 180 woredas, which are further divided

into kebeles encompassing several proximate communities or villages. Kebeles may be loosely grouped within one or more market sheds, which describe discrete areas of exchange of products along a network[45]. Horro woreda is located approximately 310 km west from the capital, Addis Ababa. Jarso woreda lies approximately 560 km east of Addis Ababa. Further details of the geography, climate, demography and agricultural practices of the two woredas are summarized in Supplementary Table 1.

Data collection

Primary data for this study were obtained from two linked studies; a rapid rural appraisal (RRA) conducted in February 2011 and a series of four repeated cross-sectional studies carried out between May 2011 and November 2012. Multistage sampling was used to select villages and participant households. Initially, two market sheds and two kebeles per market shed were selected within district in consultation with local representatives of the Department of Agriculture and local communities. For the RRA, focus group discussions (FGD) were organized comprising up to 50 farmers. We aimed to have an equal balance of male and female participants, but this was only achieved in some kebeles; female participation ranged from 20% to 50%. This may be due to a number of factors, including recruitment bias. Group discussions typically took two hours. Following the FGD, field visits were conducted in each of the kebeles to directly observe village poultry production systems. Discussions with key informants, such as district administrators and livestock extension officers were also undertaken. Data obtained through the RRA included: field notes derived from key informant and focus group interviews and during transect walks; and, quantitative data obtained through discussion and participatory exercises, including seasonal calendars and ranking and scoring of general livelihood activities, poultry

production activities and constraints, and preferred bird characteristics.

For the cross-sectional study, systematic random sampling was used to select potential participants in each kebele from list of all household heads obtained from local agricultural development agents. Each kebele was visited four times; in May/June and October/November in each year of the study (2011 and 2012). Visits were timed for before and after the main rainy season (early May or June to September). Different households were selected on each occasion (25 from each kebele in May/June and October/November 2011, and 15 from each kebele in May/June and October/November 2012; total n=640), and visited by Ethiopian staff trained to collect field samples and conduct questionnaires in the local languages. Farmers were interviewed to confirm that no exotic birds or vaccinations had been used in their flock. Moreover, since studies on poultry infectious diseases and genomics were carried out simultaneously, farmers also needed to own two indigenous birds of at least six months of age in order to be included in the study. Farmers responded to questions on management, experience of poultry disease within the previous 12 months, and on important characteristics of poultry (for details, including questionnaires and clinical examination recording sheets, see[26]).

Two chickens over 6 months of age were randomly selected from each household flock. Where possible, one male and one female were chosen. Bird ages were estimated by the owner, who also provided data on the source of the bird and how long they had owned it. Each bird was weighed, body condition scored on a 0-3 scale[46], and examined for a number of morphological characteristics (i.e. comb type, which is a mendelian trait, and plumage colour) and clinical parameters. The birds were scored for lice using a timed count of three areas of the body plus a total count of lice found under one wing and at the base of the tail

feathers[47]. Faecal samples were taken from the basket used to contain the bird or from where the bird was observed to defecate after release. Fecal samples were stored and transported in a refrigerated container to the laboratory, where they were kept at 4 °C until processed. Blood samples were collected from a wing vein into 3.2% sodium citrate, and 0.5 ml was placed on an FTA card (Whatman, GE Healthcare Life Sciences, UK). Fecal and blood samples were examined for a range of pathogens (see[48,49]). For the present study, we focused on ascarids and lice parasitism for detailed investigation as they are important pathogens of village chickens and there is scarce relevant information regarding genetic resistance. We investigated the two most prevalent gastrointestinal ascarid nematodes; *Ascaridia galli* and *Heterakis gallinarum*, the eggs of which were identified using published keys[28,50,51].

FTA cards were exported under DEFRA license (TARP/2011/245 and TARP/2012/352) to the University of Nottingham, UK. DNA was extracted from FTA cards as detailed in Smith and Burgoyne [52]. A total of 760 birds matching the phenotype described above (384 from Horro and 376 from Jarso) with detailed phenotypes were genotyped using a genome-wide high density (600K) single nucleotide polymorphism (SNP) array (A☐ymetrix® Axiom® HD)[53].

An additional 200 households, 25 in each kebele, were visited during the first round of surveys in May 2011. Selection of these households was identical to that described above, but without the criterion that required them to currently own two adult indigenous chickens. These households only completed the survey relating to the social and economic aspects of chicken keeping.

Data analysis

Data obtained during the farmer questionnaire surveys were analyzed using descriptive

statistics and comparisons between woredas were made using chi-squared tests for

categorical data and Mann-Whitney tests for continuous data (which was almost universally

non-normally distributed). Prior to analysis, data on livestock holdings in each household

were converted to a Tropical Livestock Unit (TLU) following Storck et al.[27]. TLUs adjust for the

size and weight of species kept and facilitates comparison between individuals and areas.

Parasite aggregations were calculated using the corrected moment estimate, k,[54] and the

index of discrepancy[55]. Parasite aggregation was compared between woredas using

Kolmogorov-Smirnov tests. Factors associated with bird-level characteristics were identified

using mixed effects regression analysis in the lme4 package[56]. Analyses were performed

using R version 3.2.2[57]. Field notes collected during the rapid rural appraisal were analyzed

using thematic analysis. Data from the ranking and scoring exercises were tabulated for each

woreda.

Climatic conditions between each region were compared using ecological niche modelling[58],

which applied the climatic conditions of each region to make predictions of the potential

distribution of the ecotype found in one region onto other regions. We used the maximum

entropy algorithm implemented by Maxent, which estimates the distribution probability of a

species using occurrence data, and a set of environmental predictors[59] that are commonly

used as indicators of annual trends in seasonality, temperature and precipitation[60]. Initially,

we modelled the current potential distribution of each population using 21 environmental

variables at 1 km x 1 km resolution as predictors of habitat distribution. As indicators of

climatic tolerances, 19 bioclimatic variables and one elevation layer obtained from

WorldClim[60] were used. As chicken production is linked to smallholder farming[2], we used a

land cover variable as a proxy to agricultural systems, share of total cultivated land, obtained

from the Harmonized World Soil Database v1.2[61]. We used the default settings and additionally selected the minimum training presence threshold and the logistic output format, which generates a probability of occurrence that ranges from 0, low probability of occurrence, to 1, high probability of occurrence, making it easier to interpret. Then, to evaluate if the model for each population would classify as climatically suitable areas where the other ecotype is located, we projected the generated models of each ecotype onto the geographic area of the other. To not restrict our analyses to the woreda administrative boundaries, we extended each area 50 km in all directions. We validated the models using the receiver operating characteristic (ROC) curve and a binomial test of omission (40). The analyses were developed within R version 3.2.2[57] using the dismo package[62]

For the selective sweep analysis, 760 chickens (384 from Horro and 376 from Jarso) and 391,384 SNPs that passed the quality control (see Desta[63] for details) were used. The R package rehh[64] was used to map selective sweeps of genetic markers subjected to moderate selection pressure using iHS statistics, while SweeD[32] was used to identify candidate genomic regions that have been subjected to strong selection at intra-population level. The same birds and genotyping data as for the selective sweep analysis were used in GWAS analyses together with relevant phenotypes to detect SNP markers associated with resistance to ascarids and lice parasitism as well as rose versus simple comb. Multidimensional scaling analysis was performed to identify if the two populations were distinct and if further population substructure was present using the GenABEL package of R[65]. This identified two distinct populations that exactly matched the origin of the birds (in Horro or Jarso; Supplementary Figure 4). GWAS analyses for disease traits were performed using the PLINK v1.9[66] and GEMMA v0.94[67] software and the univariate linear mixed model described

previously by Psifidi et al.[25]; while GenABEL package[65] was used to map genomic regions associated with the rose comb phenotype (for details see Desta[63]). After Bonferroni correction for multiple testing, the significance thresholds were set at $P \leq 1.2 \times 10^{-7}$ and $P \leq 2.5 \times 10^{-6}$ for genome-wide ($P \leq 0.05$) and suggestive (one false positive per genome scan) levels, respectively. The candidate regions harboring the genes and mutations responsible for resistance to ascarids and lice parasitism, as well as rose comb, were defined as the genomic intervals 100kb upstream and downstream of the significant markers identified in GWAS, based on the average linkage disequilibrium estimated for the two indigenous ecotypes[25]. The candidate genomic regions for disease traits and rose comb mutation identified in GWAS analyses were compared with targets of signatures of selection in the same data. We used the BioMart data mining tool within the Ensembl genome browser (http://www.ensembl.org/biomart/martview/) and the Galgal5 assembly of the chicken reference genome to identify the genes located in the candidate genomic regions for rose comb, ascarids and lice parasitism resistance, as well as in selective sweep regions.

Data availability

The bioclimatic variables that used in this study are available in "WorldClim" (http://www.worldclim.org/). The land cover variable data is available in "Harmonized World Soil Database" (http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML/index.html?sb=1). All other data that support the findings of this study are available from the corresponding author upon reasonable request to the corresponding author.

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Competing Interests

The authors declare not competing interests.

Figure Legends

Fig. 1. Location of the study regions (a; red shape indicates Horro, blue shape Jarso) and potential distribution models constructed separately for each breed and projected onto the other. Models of the potential distribution for each ecotype were constructed separately for each study region based on the bioclimatic variables measured in the other study region. The district map for Horro (b) displays the modelled potential distribution of Jarso birds (indicated by the blue shading) and *vice versa* for Jarso (c). Darker shading denotes areas of greater climatic similarity. Note that each area has low predicted similarity according to the model built with data from the other population, suggesting climatic dissimilarity. The environmental variables that contributed the most to the model for Horro were *Precipitation of Wettest Month* (49.2%) and *Temperature Seasonality* (27.2%), and for Jarso were *Temperature Annual Range* (38.7%) and *Precipitation of Wettest Month* (23.2%). Hence, the Horro ecotype is kept in, and may be adapted to, areas with higher precipitation and less temperature seasonality, with higher precipitation in the wettest and driest periods compared to the Jarso ecotype.

Fig. 2. Ownership and usage of chickens (median value; within previous 12 months) in the

two study regions, (a) Horro and (b) Jarso, Ethiopia, for different categories of household income. Although ownership of chickens is similar in both regions, utilization of chickens was greater in Horro, where there was evidence of increasing utilisation with increasing income. Data from 200 households in Horro and Jarso woreda in Ethiopia (total n = 400). See Supplementary Table 7 for detailed summary data. (ETB Ethiopian Birr).

Fig. 3. Household income from chicken production in two regions of Ethiopia. Income from chicken production tended to contribute a greater proportion of family income in poorer households in both regions (a). However, a smaller proportion of the poorest families derived income from their chickens compared to wealthier households (a). Points in (a) are scaled relative to the number of breeding female chickens owned. Data from 200 households in Horro and Jarso woreda in Ethiopia (total n = 400).

Fig. 4. Manhattan plots displaying the genome-wide association analysis results for ascarid and lice infection in two regions of Ethiopia (Horro and Jarso). Genomic location (horizontal axis) is plotted against $-\log_{10}(P)$; genome-wide ($P < 0.05$, after adjusting for multiple testing with Bonferroni correction) and suggestive genome-wide thresholds are shown as red and blue lines, respectively.

Fig. 5. Sustainable chicken production intervention framework. Sustainable chicken production operates within a zone defined by inputs and outputs. The sustainable zone is delineated by regions that are unsustainable (where inputs exceed outputs) or unattainable (where outputs cannot be attained with given inputs). Within the sustainable zone, efficiency of production can be achieved by increasing outputs relative to inputs. Three examples of strategies toward enhanced production efficiency as illustrated.

Table 1. Household demographics and utilization of chicken assets in the two study regions, Horro and Jarso, Ethiopia. Data were obtained from 200 randomly selected households per region, collected in May 2011. Quantitative (numerical) variables reported as median [inter-quartile range]. Categorical variables reported as number (percentage: 95% Confidence Interval), unless otherwise indicated.

Variable		Horro	Jarso	P value
Household head age (years)		38 [30.0-55.0]	35 [30.0-47.8]	0.07[*]
Female-headed households		16 (8%: 5-13%)	10 (5%: 3-9%)	0.3[†]
Family size (number of people)		7.0 [5.0-8.0]	6.0 [5.0-8.0]	0.1[*]
Household head education level[§]	None	37%	63%	<0.001[‡]
	Primary	42%	35%	
	Secondary	13%	1%	
	High school	7%	1%	
	College	1%	0%	
Household land size (Ha)		2.0 [1.0-3.0]	0.4 [0.3-0.5]	<0.001[*]
Chicken ownership[¶] (% [95%CI])		75% [67-82%]	71% [63-77%]	0.5[†]
TLU[#] owned		7.6 [4.3-11.5]	2.1 [1.2-3.2]	<0.001[*]
Chicken TLU[#]		0.21 [0.10-0.36]	0.10 [0.06-0.16]	<0.001[*]
Chicken number		8.0 [4.0-14.25]	4 [2-6]	<0.001[*]
Reported value of flock (ETB)		173 [98.5-265]	75 [40-115.8]	<0.001[*]

Purpose of chicken keeping	Sale	181 (96%: 93-98%)	175 (93%: 88-96%)	0.18[†]
	Consumption	69 (37%: 30-44%)	35 (19%: 14-27%)	<0.001[†]
Purpose of egg production	Hatching	131 (70%: 63-76%)	60 (30%: 24-37%)	<0.001[†]
	Sale	76 (41%: 34-48%)	131 (66%: 59-72%)	<0.001[†]
	Consumption	47 (25%: 19-32%)	61 (31%: 25-37%)	0.27[†]
Sold chickens in last 12 months		114 (57%: 50-64%)	76 (38%: 32-45%)	<0.001[†]
Number of chickens sold[‡]		4 [2 -6]	2 [1-4]	<0.001[*]
Sold eggs in last 12 months		17 (8.5%: 5-13%)	37 (18.5%: 14-24%)	0.005[†]
Income from sale of chickens in past year (ETB)[‖]		120 [70 -220)	56 [30 -100]	<0.001[*]
Percentage of household income from chickens [‖]		1.68 [0.96 – 2.85}	0.68 [0.39 – 1.49]	<0.001[*]
Mean (sd) price per hen (ETB)		26 (14)	17 (5)	<0.001[*]
Mean (sd) price per cock (ETB)		41 (14)	27 (12)	<0.001[*]
Eaten chickens in last 12 month		132 (68%: 61-74%)	35 (18%: 13-23%)	<0.001[†]
Number of chickens consumed[Δ]		2 [1-3]	3 [2-4]	0.054[*]
Eaten eggs in last 12 month		33 (17%: 12-22%)	45 (23%: 17-29%)	0.165[†]
Number of eggs consumed [Δ]		20 [10-40]	21 [12-50]	0.33[*]

[*] Mann-Whitney U test

[†] Chi-square test

[‡] Chi-square test for trend

[§] Primary (grade 1-4), Secondary (grade 5-8), High school (grade 9-12).

[¶] estimated from number of households not owning chickens among all households that were visited to identify the required number owning at least 2 adult birds

[#] TLU – Tropical Livestock Units, calculated according to Storck *et al* (26).

[‖] Calculations based on households which sold at least 1 chicken or egg (as appropriate)

[Δ] Calculations based on households which consumed at least 1 chicken or egg (as appropriate). Among the entire sample, the median number of chickens consumed per household in the last 12 months was 1 in Horro and 0 in Jarso (see also Figure 2), and 0 eggs in both Horro and Jarso.

ETB = Ethiopian Birr. At the time of the study, 1 USD was approximately equal to 17 Ethiopian Birr (ETB)

Horro

a

Jarso

b

Median number of chickens

Owned
Eaten
Sold

Income (ETB)

<2500   2500–5000   5001–7500   7501–10,000   10,001–15,000   >15,000

a

Annual household income
(Ethiopian Birr)

Percentage of household income

- Horro (red)
- Jarso (blue)

- 50 ETB
- 100 ETB
- 200 ETB

b

Proportion of households
obtaining no income
from poultry
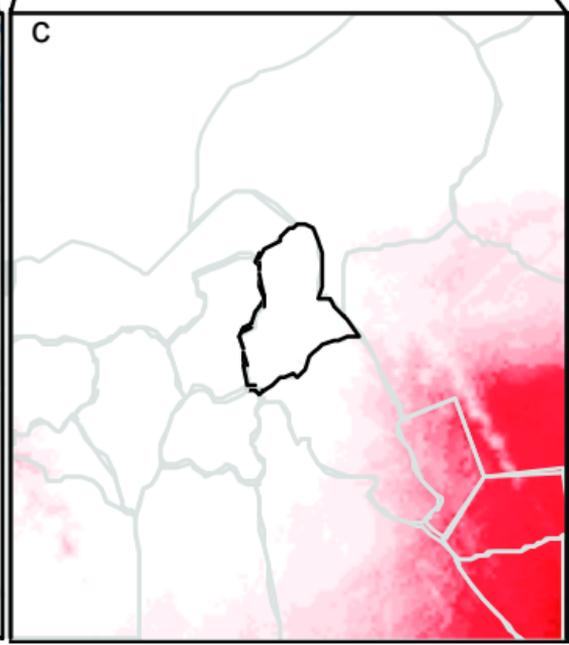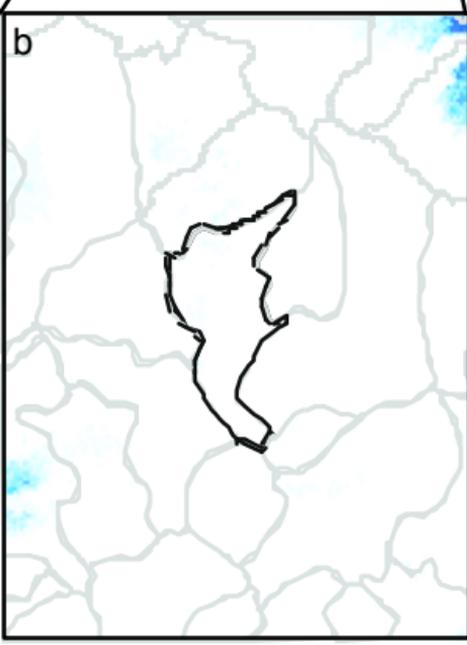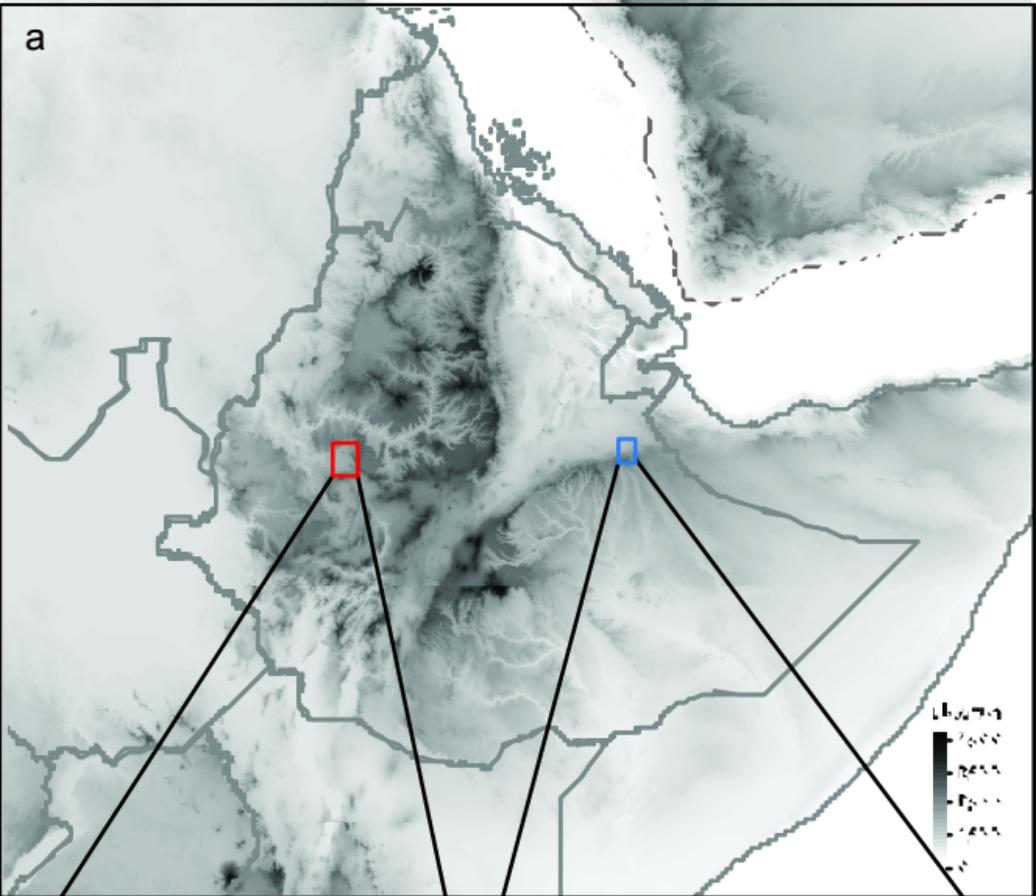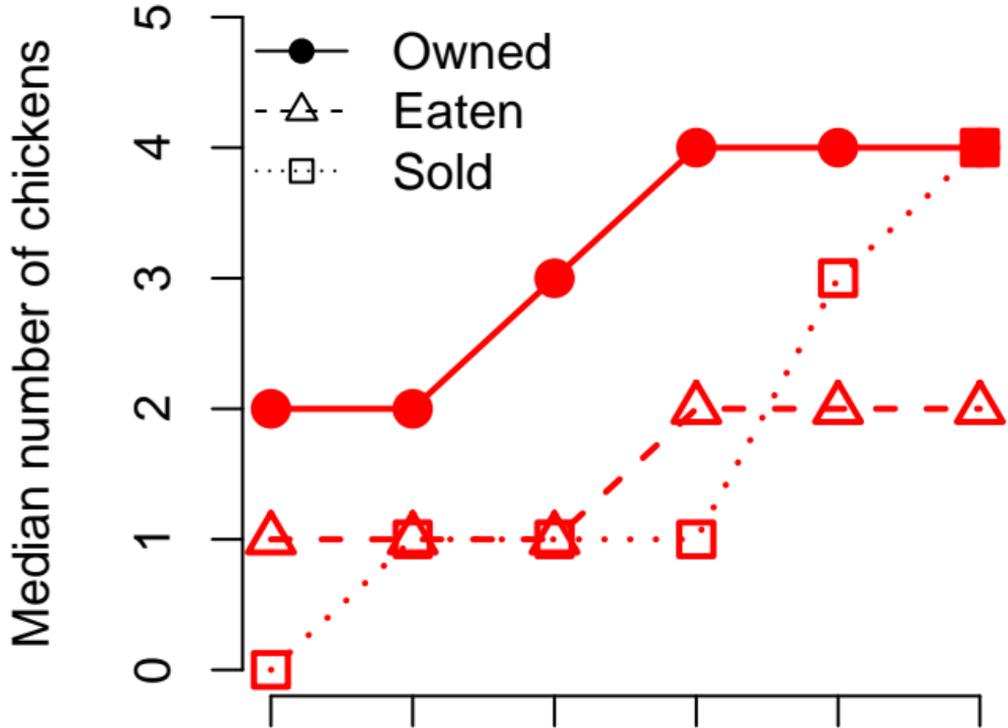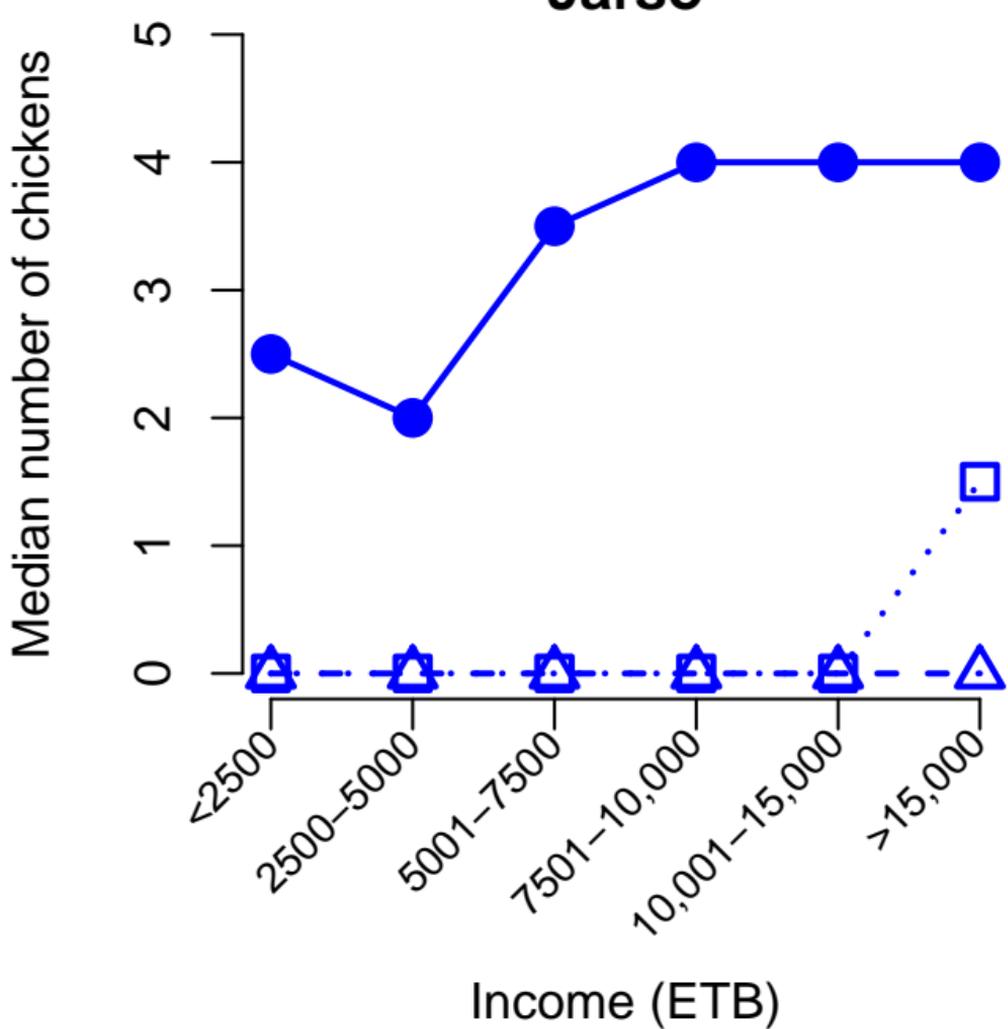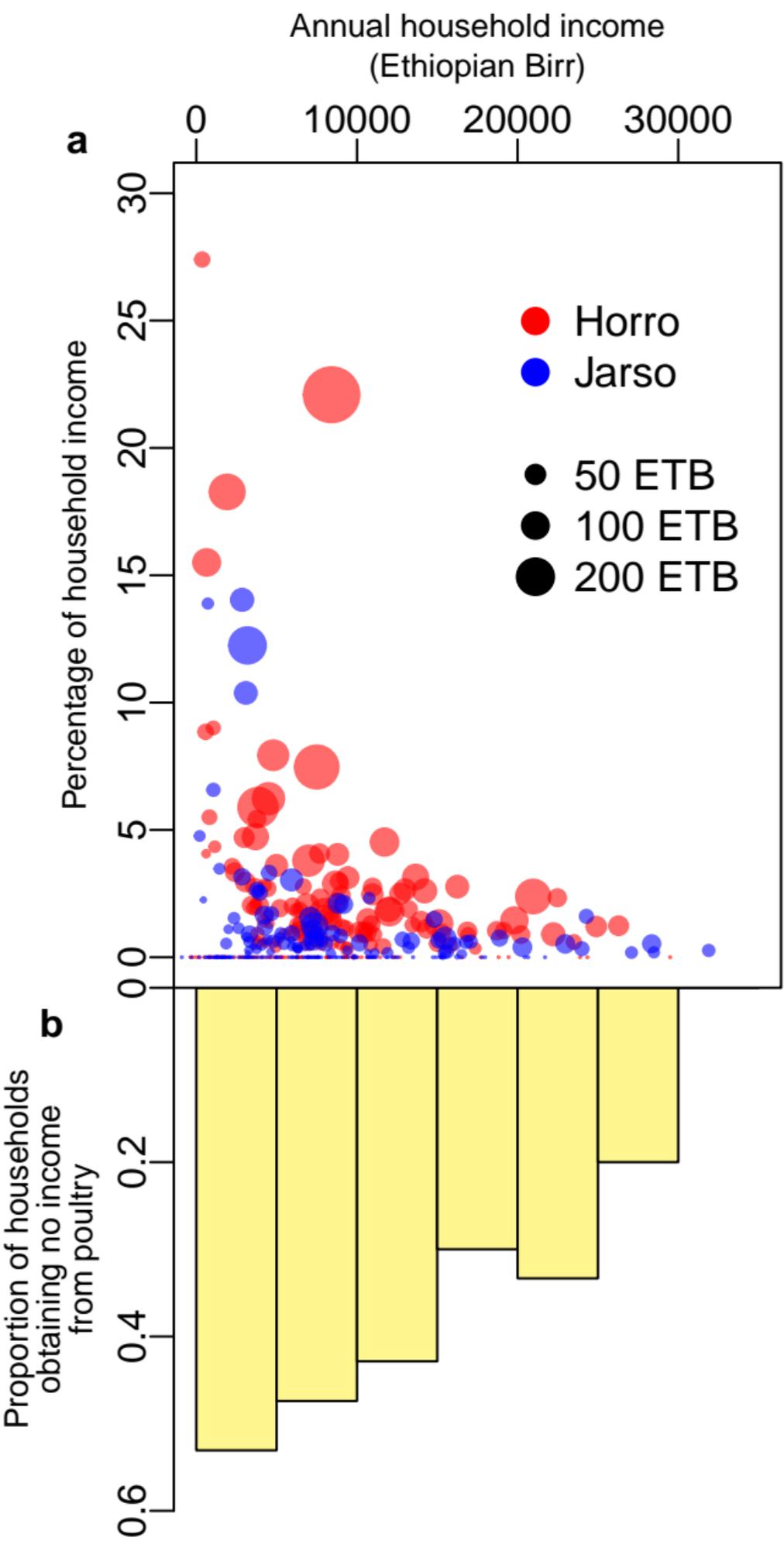
Ascarids in Horro chickens
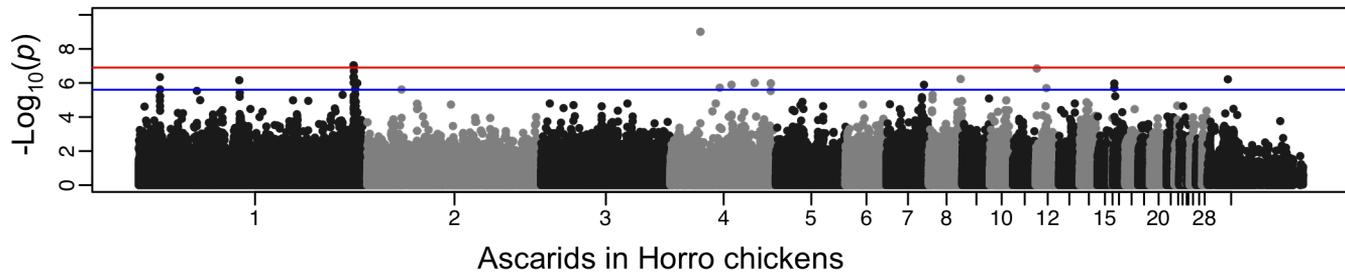
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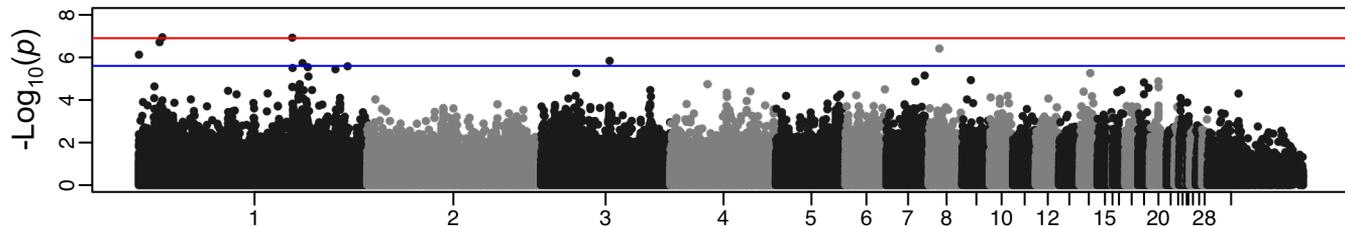
Lice in Horro chickens
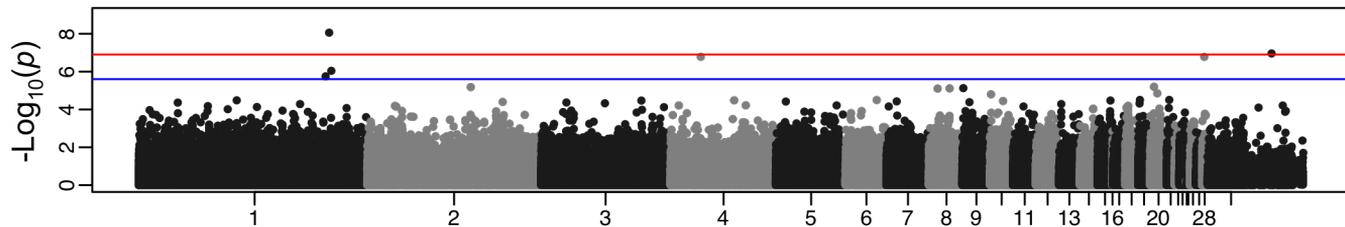
Lice in Jarso chickens
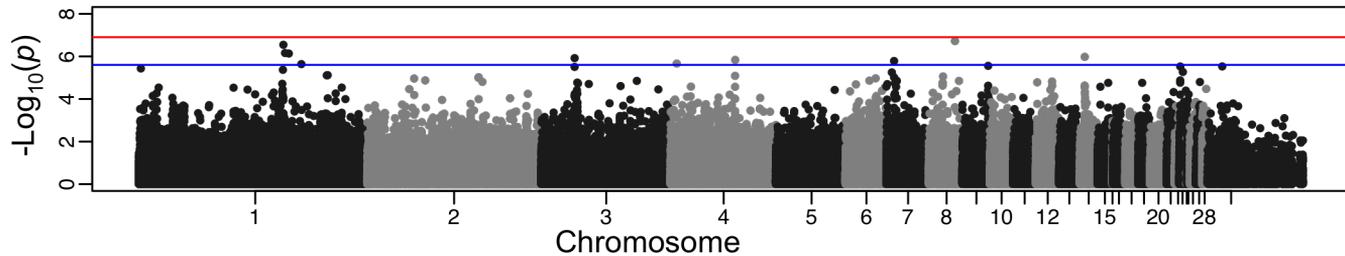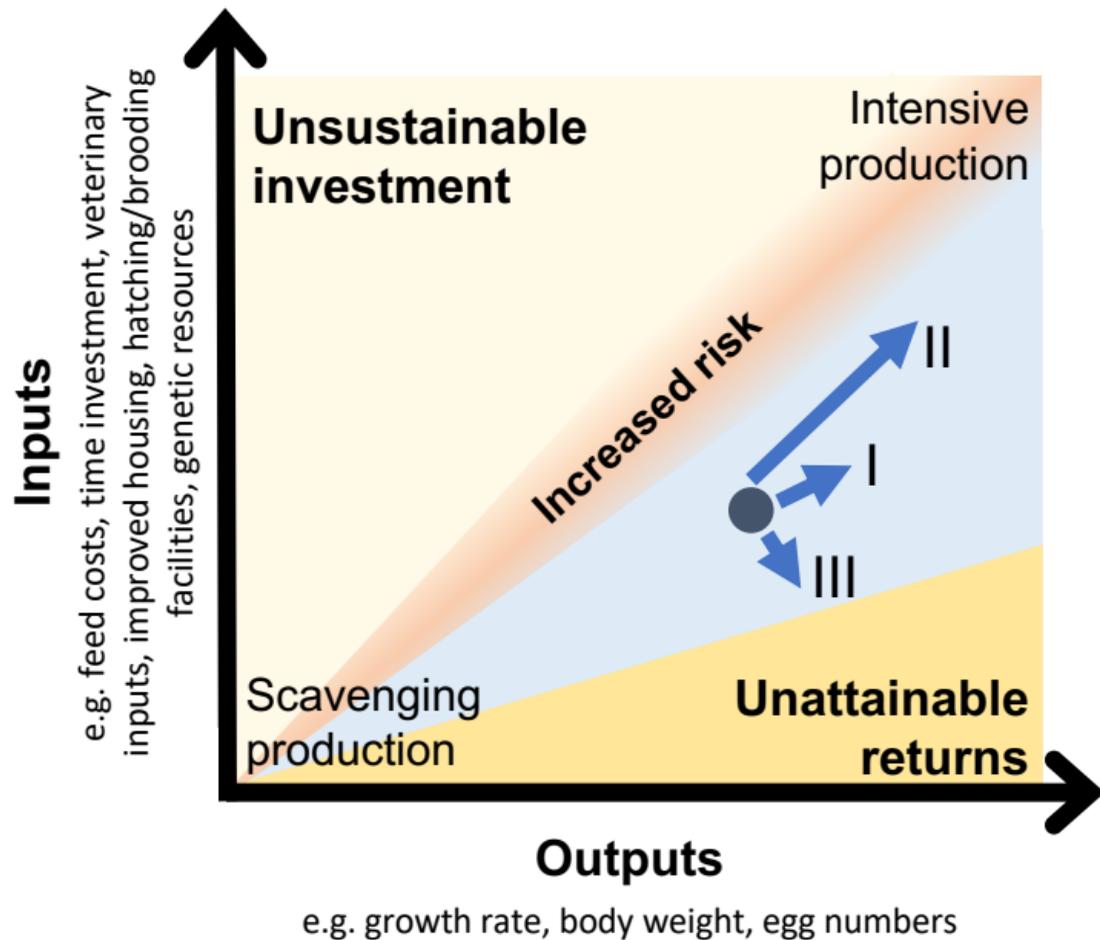
Example trajectories:

I) Small increase input to realize increased output: e.g. vaccination resulting in reduced losses due to disease, or; supplementary feeding to enhance growth.

II) Markedly increased output through considerably increased input (and risk): e.g. semi-intensification of production, or; heavy selection for production traits.

III) Maintained, or slightly increased, output but decreased inputs: e.g. destocking over the high disease-risk rainy season to reduce supplementary feed requirements.