



New perspectives on the ecology of early domestic fowl: An interdisciplinary approach



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ABSTRACT

Introduced into Europe during the Bronze- and Iron Ages as an exotic, non-native species, very little is currently understood about the origins and spread of early domestic fowl, *Gallus gallus domesticus*. Ecological niche modelling of extant Red Junglefowl, *Gallus gallus*, presents a unique opportunity to examine historical ecological implications associated with its descendant, the chicken, in early stages of domestication. We model the environmental conditions associated with Red Junglefowl populations both in south-east Asia, where the bird originates, and populations transported further afield as a consequence of human interaction. This allows us to establish the full extent of the ecological tolerance of the ancestor bird. We show that potential for suitable sets of environmental conditions for Red Junglefowl in Europe ranges from poor to limited, based on both current climate and when projecting to mid-Holocene (ca. 4000BCE) climate simulations. This suggests that human intervention played a vital contribution during early domestication to ensure the future widespread success of the chicken. These conclusions offer new insights into the archaeological evidence. We identify areas in the native range as the probable location of first domestication, and not China as has been suggested. We suggest that a dispersal route into Europe via the Mediterranean offers the best ecological potential to aid survival for a recently domesticated version of this species. Identifying the environmental tolerances of Red Junglefowl may also aid future conservation of this species, now highly endangered in its true wild form.

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1. Introduction

With a population of over 20 billion (Chemnitz and Becheva, 2014) and near global distribution, the domestic fowl or chicken *Gallus gallus domesticus* is the most widespread domestic animal. Chickens have influenced many facets of human life, including ritual, religion, culture, and identity; in addition to their more commonly recognised uses as producers of meat, eggs and feathers. While it is widely accepted that domestic fowl are descended from junglefowl, very little is understood regarding their origins and dispersal around the globe. Despite the success of the chicken, the junglefowl has also survived, offering an excellent opportunity to examine the ancestor in order to explore issues faced by recently domesticated species, including responses to new environments and the corresponding implications of animal husbandry.

There are four extant species of junglefowl, namely Red

Junglefowl, *Gallus gallus*; Grey Junglefowl, *Gallus sonneratii*; Sri Lanka Junglefowl, *Gallus lafayetii*; and Green Junglefowl, *Gallus varius*. Originating in Southern and Southeast Asia, India and Indonesia, and predominantly occupying tropical rainforest environments, they have historically been confined to this range by geographical barriers (Fig. 1).

There are very few archaeological specimens found outside of the native range which are identified as Red Junglefowl, rather than chicken; although whether this is because bones bearing *Gallus* traits are automatically identified as chicken in areas outside the native junglefowl range is unclear. Early chickens are often noted to be of similar size to Red Junglefowl. Junglefowl (and chickens), however, are non-migratory with limited flight capability, rendering mountains and large bodies of water impassable. Inhospitable environments such as desert or semi-desert lacking corridors of environmental suitability further restrict natural dispersal to areas which would otherwise be suitable. Red Junglefowl have been transported by humans to most continents in more recent times, but there are no reported occurrences of the other three species outside their native ranges. Of the four junglefowl

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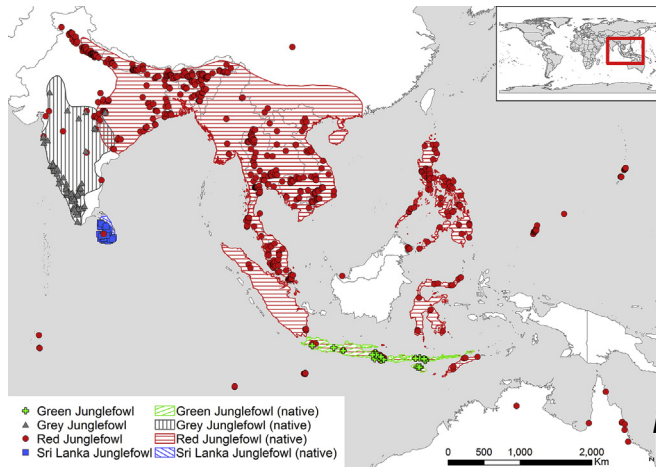


Fig. 1. Geographic range (hatched area, IUCN Redlist) with occurrence points (GBIF.org) for all four junglefowl species.

species, genetic studies have identified the contribution of the Red- and Grey Junglefowl to the domestic mix. Red Junglefowl is the dominant ancestor for early domestic fowl, with hybridization with Grey Junglefowl occurring millennia later. (Eriksson et al., 2008; Girdland Flink et al., 2014).

As yet, there is no clear chronology for the early domestication of the chicken, largely due to potential misidentification of the remains, lack of secure context or poor dating evidence (Harrison, 1980; Stewart, 2005, 2007; Bochenski, 2008). Multiple rather than single origins of domestication are now accepted (Liu et al., 2006; Kanginakudru et al., 2008; Xiang et al., 2014), with mtDNA providing support for localised domestication events in South Asia, Northeast India, Southwest China, and a further event in Southwest China and Southeast Asia (Miao et al., 2013). The earliest proposed domestication event is Nanzhuangtou, China ca. 8050BCE (Xiang et al., 2014); but this has been contested (Peters et al., 2015; Xiang et al., 2015; Eda et al., 2016). Eda et al. (2016) recently reappraised evidence at other early Chinese sites (West and Zhou, 1988) concluding that the earliest specimens are not chicken, but one or more of the other 53 Phasianidae species found in China. This leaves the oldest evidence from a secure archaeological context found in Asia at Harrapan Culture sites in the Indus valley, India, ca. 2500BCE (Zeuner, 1963; Fuller, 2006).

An eastward expansion of the domestic chicken via Oceania to South America has been demonstrated using archaeological evidence (Storey et al., 2007, 2008; Fitzpatrick and Callaghan, 2009) and DNA analysis (Gongora et al., 2008; Storey et al., 2012; Thomson et al., 2014). Despite its archaeological relevance as a proxy for human dispersal and cultural associations, there has been less consideration of its route westwards and into Europe, largely due to a lack of collated zooarchaeological evidence. Routes proposed include dispersal into Europe by way of a northern route into China, spreading to Europe via Russia (West and Zhou, 1988); or west via Phoenician trade routes (Becker, 2013). These correspond with some of the earliest proposed evidence outside of Asia, including Bulgaria, ca. 5550BCE (Boev, 2009), the Southern Levant, ca. 2500BCE (Perry-Gal et al., 2015) and Iberia, ca. 2000BCE (von den Driesch, 1973). Recent literature highlighting issues with other early evidence (Kysely, 2010; Peters et al., 2015), suggests that these unusually early dates for European sites may require verification. Evidence is present in secure archaeological contexts from at least the Iron Age in Europe, ca. 500BCE (Hamilton, 2000; Kysely, 2010; Strid, 2015). Placing archaeological evidence in the context of environmental suitability can be used to aid interpretation of these

early specimens.

Ecological niche models (ENM) are frequently used in ecological research to better understand the environmental conditions that enable a species to persist. They predict the presence of suitable conditions, but not where the species will necessarily be found. Estimating the latter benefits from consideration of biotic and geographical factors, which falls outside the scope of ENM and this study. Various methods exist for performing ENM. However, maximum entropy modelling (Maxent) has been demonstrated to work well with presence-only data,¹ such as the data available for this study (Phillips et al., 2004; Elith et al., 2006; Banks et al., 2013). It is a machine learning method which takes the average value for a set of random sample points within a calibrated region (study area where the species is found and able to survive within geographical boundaries and environmental tolerance). It calculates how this differs from known sets of environmental values at locations the species is known to occur to estimate the probability of occurrence given particular environmental conditions. This can then be projected to other regions of the world or other time-periods (Phillips et al., 2006).

Modelling the ecological niche of Red Junglefowl enables evaluation of how far the chicken today has conserved or shifted its fundamental niche. The fundamental niche indicates where the species can survive, as opposed to the realised niche, which relates to where the species is actually found. The former is of most importance to this study. Wild populations within the region of origin may not represent the full fundamental niche of the species. Geographical barriers limiting movement mean that any niche based on these observations more closely reflects a realised niche and ENM enables us to predict the consequences of removing these barriers to movement. Comparing the niches of native wild populations to populations which are known to have already been transported by humans to locations that would otherwise be geographically inaccessible, identifies how well Red Junglefowl acclimate to different environments and latitudes. The combination of both niches establishes the full suite of environmental tolerance for this species, including those that have been subject to human interaction and, inevitably, some level of artificial selection. Higher environmental suitability values indicate where the species is more likely to be able to survive and breed. First domestication of a species in an area of poor environmental suitability is unlikely to be successful. Lower suitability would necessitate increased assistance by other means, i.e. direct (feeding and housing) or indirect (selection during breeding) human intervention. The earliest examples of domestic fowl would have had limited chance to evolve distinct physiological and morphological traits from their ancestor. Therefore, identifying potential for suitable environmental conditions at archaeological sites with early evidence of chicken can inform not only the likelihood for the site being a location of first domestication, but also the extent of human effort required during early domestication to ensure survival of this newly domesticated, exotic species.

2. Materials and methods

ENM input requires a dataset of occurrence points and environmental variable layers for the relevant geographic extents.

We used observation data for Red Junglefowl post-1950 downloaded from the Global Biodiversity Information Facility (GBIF.org (11th February 2016)). Observations which were described as domestic, were unclearly georeferenced, exact duplicates, or were located outside of the boundary of the global terrestrial

¹ As opposed to data with known presences and confirmed absences.

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