Previous studies have shown that ticks (Figure 1) have very low metabolic rates relative to other arthropods (Lighton & Fielden, 1995), a necessary condition for long-term starvation survival. Somewhat surprisingly, Rosendale et al. found that metabolic rates tended to increase over time, probably because ticks became more sensitive to environmental conditions (e.g., an experimenter’s breath) that might indicate the presence of a host. Activity and questing behaviour (assuming a posture that allows a tick to rapidly latch on to a passing host) increased as starvation progressed. Another energy-requiring process is uptake of water vapour. Ticks do not drink between meals and therefore must replace water lost via respiration and the cuticle by active absorption of water vapour (Benoit & Denlinger, 2010). Perhaps ticks cannot lower their metabolic rates during starvation because they are already at the lower limits of metabolism.

Rosendale, Dunlevy, Marshall, and Benoit (2018) also investigated which energy sources ticks consumed to support metabolism. Lipids provided the primary source of ATP in the first month, with the lipid content per tick declining by 65% after 4 weeks. In subsequent months, lipids continued to decline slowly, but not significantly relative to overall dry mass. Glycogen levels dropped...
substantially, but quantitatively contributed only a minor amount to metabolism. Instead, long-term starvation appeared to be fuelled by protein catabolism. Molecular data described below support this idea.

The physiological and behavioural data reveal that ticks are not just sitting-and-waiting between meals, but are changing over time. Rosendale et al. (2018) used RNA-seq to generate whole-tick transcriptomes up to 36 weeks post-moult, when significant mortality began to set in. The first problem to be addressed was that the genome of *D. variabilis* has not been sequenced, and existing tick genomes are not of particularly high quality (Gulia-Nuss et al., 2016). Rosendale et al. used two methods to generate de novo transcriptome assemblies which were then combined. Over 40,000 contigs were generated, about half of which matched proteins in the NCBI arthropod nr database. Like any ‘omics study of a non-model organism (and often for model organisms), the conclusions should be taken with a grain of salt.

The largest changes in gene expression occurred between 1 and 4 weeks post-mouling. Using three separate gene ontology enrichment tools, Rosendale et al. (2018) found over 200 genes each that were consistently up-regulated or down-regulated relative to Week 1. Up-regulated genes included those in GO categories such as ribosome biogenesis, protein catabolism and RNA processing, while down-regulated genes were enriched in peptidase inhibitors. Many additional genes in these categories appeared in pairwise comparisons between transcriptomes of ticks after 4–36 weeks post-moult.

Following an overall analysis of the pattern of transcriptome changes, Rosendale et al. focused their attention on a few specific categories expected to be particularly relevant to tick ecology: genes associated with autophagy, chemoreception and immune function, as well as genes expressed in salivary glands. Autophagy genes were chosen because of physiological data suggesting catabolism of proteins in long-term starvation. Ionotropic chemoreceptors have been implicated in host sensing, and immune responses are required once a tick does feed (Gulia-Nuss et al., 2016). Salivary gland genes were selected to determine whether ticks might prepare for feeding during long-term starvation, even before they detect a host.

Previous studies had suggested that at least some ticks catabolize proteins between meals; this study confirms this for dog ticks and finds supporting molecular evidence. Over 300 autophagy-related contigs were differentially expressed during starvation. Of special interest were seven that were directly involved in autophagy (as opposed to regulation of the process). Two of these increased rapidly in expression from Week 1 to Week 7, while the other five showed consistent increases in expression through 36 weeks. Overall, changes in autophagy-related gene expression, as well as decreases in peptidase inhibitors, were consistent with protein catabolism during starvation, suggesting that this is part of the normal tick starvation response. While gustatory receptors did not change in expression, 5 of 19 contigs annotated as ionotropic receptors did. Although these expression differences could be somewhat inconsistent, three of the putative ionotropic receptors were most highly expressed after 36 weeks of starvation. If these are indeed related to host detection, these changes in gene expression are consistent with the increased questing behaviour as starvation continues. More consistent patterns were noted for immune function and salivary gland genes. Both categories showed generally increased expression as starvation progressed. These changes suggest a progressive readiness for consuming their next meal.

The picture emerging from this study is one of relatively slow changes during long-term starvation. Ticks are not in stasis until the next meal literally walks by, but are making physiological adjustments over time. They switch to protein catabolism as lipid reserves decline, they become more proactive in their foraging behaviours, and they prepare biochemically to consume their next meal. These patterns are consistent with the observed transcriptome changes, but much remains to be done. Rosendale et al. used whole ticks for their work; tissue-specific studies are needed. For example, are the changes in ionoreceptor expression associated with Haller’s organ, the tick’s CO₂-sensing structure? What are the neurological changes underlying increased foraging activity? And for this physiologist, what are the molecular mechanisms underlying the salivary glands’ role in water vapour uptake?

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